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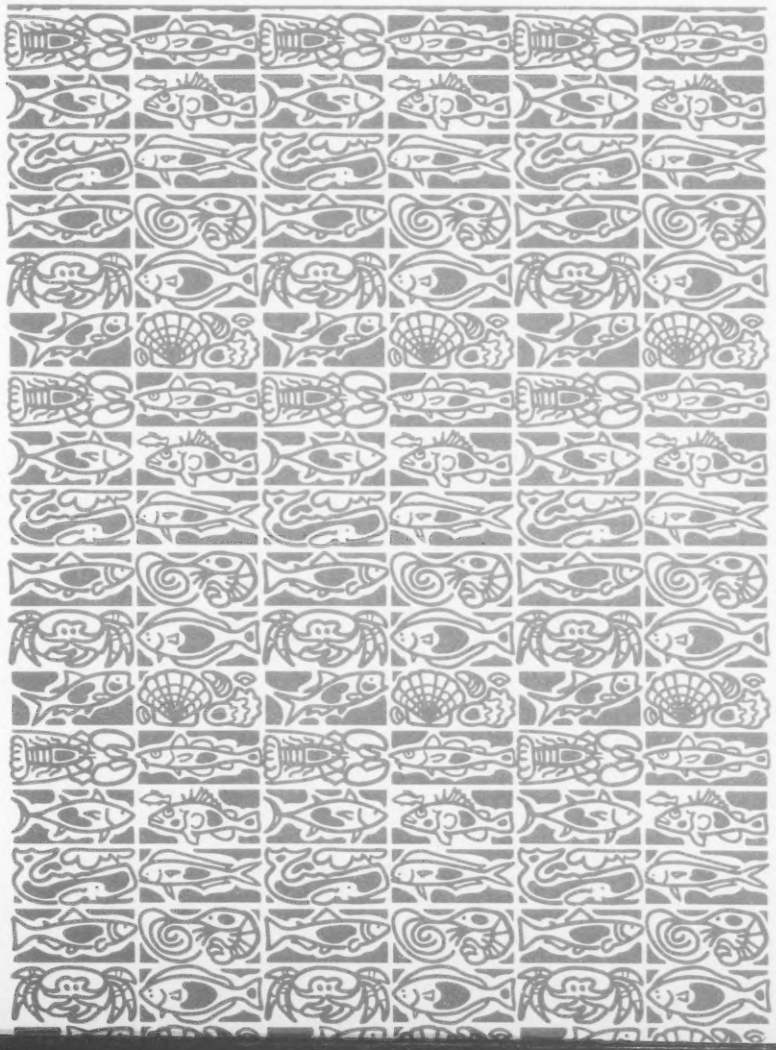

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Volume 100
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Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus thynnus*), in relation to oceanographic conditions of the western North Atlantic, determined with ultrasonic telemetry

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Abstract—We employed ultrasonic transmitters to follow (for up to 48 h) the horizontal and vertical movements of five juvenile (6.8–18.7 kg estimated body mass) bluefin tuna (*Thunnus thynnus*) in the western North Atlantic (off the eastern shore of Virginia). Our objective was to document the fishes' behavior and distribution in relation to oceanographic conditions and thus begin to address issues that currently limit population assessments based on aerial surveys. Estimation of the trends in adult and juvenile Atlantic bluefin tuna abundance by aerial surveys, and other fishery-independent measures, is considered a priority.

Juvenile bluefin tuna spent the majority of their time over the continental shelf in relatively shallow water (generally less then 40 m deep). Fish used the entire water column in spite of relatively steep vertical thermal gradients (≈24°C at the surface and ≈12°C at 40 m depth), but spent the majority of their time (≈90%) above 15 m and in water warmer then 20°C. Mean swimming speeds ranged from 2.8 to 3.3 knots, and total distance covered from 152 to 289 km (82–156 nmi). Because fish generally remained within relatively confined areas, net displacement was only 7.7–52.7 km (4.1–28.4 nmi). Horizontal movements were not correlated with sea surface temperature. We propose that it is unlikely that juvenile bluefin tuna in this area can detect minor horizontal temperature gradients (generally less then 0.5°C/km) because of the steep vertical temperature gradients (up to ≈0.6°C/m) they experience during their regular vertical movements. In contrast, water clarity did appear to influence behavior because the fish remained in the intermediate water mass between the turbid and phytoplankton-rich plume exiting Chesapeake Bay (and similar coastal waters) and the clear oligotrophic water east of the continental shelf.

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Fish. Bull. 100:155–167 (2002).

Current estimates of spawning biomass for Atlantic bluefin tuna (*Thunnus thynnus*) remain controversial (Butterworth and Punt, 1993; Restrepo et al., 1994; Restrepo, 1996), although the most conservative predicts that a population eight times the current size would be needed to produce maximum sustainable yields (Sissenwine et al., 1998). The current strict catch quotas are based on abundance assessments for both adult and juvenile (i.e. "schooling") fish (age classes 1–5 years, body mass ≈6–60 kg). Adult abundance is derived from commercial landings data; juvenile abundance has, since 1985, been based on fishing effort and landings data obtained from dockside intercepts and telephone polling of the largely recreational fishery for juvenile bluefin tuna conducted by the National Marine Fisheries Service's Large Pelagics Survey (Turner et al., 1993, 1997). The usefulness of both data sets can be compromised, however, because the relationship between catch-per-unit-of-effort (CPUE) data and real abundance is not known with certainty (Bakun et al., 1982; Hilborn and Walters, 1992; Lauck, 1996). This problem is especially critical with highly mobile schooling fishes like tunas because of environmental influences on fish distribution and vulnerability to specific fishing gears, as well as the introduction of new fishing techniques (Sharp, 1978; Clark and Mangel, 1979; Brill, 1994; Bertrand and Josse, 2000).

Juvenile Atlantic bluefin tuna appear in the surface waters off the east coast

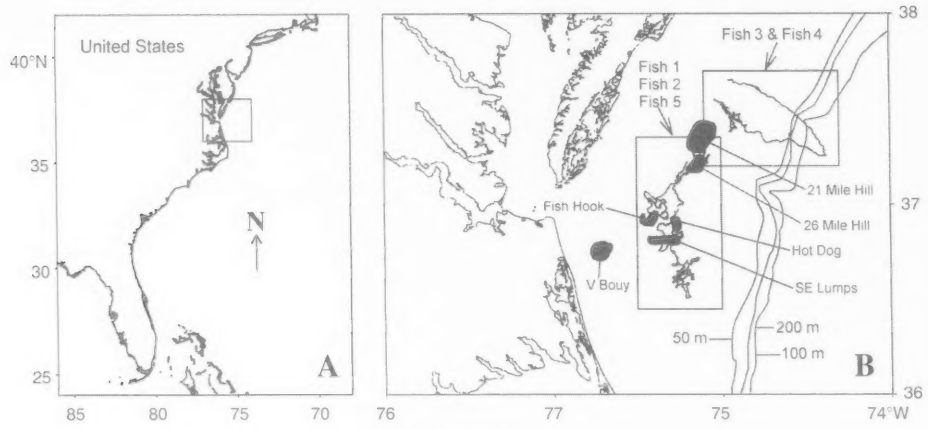

Figure 1

(**A**) Map of the east coast of the United States. The rectangle shows the area enlarged in panel B. (**B**) Movements of five juvenile bluefin tuna (*Thunnus thynnus*). The limit of the continental shelf is shown by the 50-, 100-, and 200-m isobath lines. The topographic features considered by local fishermen to aggregate juvenile bluefin tuna are shown by the shaded areas. Place names are taken from local fishing charts. The rectangles show the areas enlarged in Figures 3 and 4.

of the United States, from North Carolina to Rhode Island, usually during June and July (Rivas, 1978; Sakagawa, 1975; Roffer, 1987; Lucy et al., 1990; Mather et al., 1995). Their presence provides an opportunity for direct population assessments with aerial surveys similar to those conducted on adult Atlantic bluefin tuna (Lutcavage and Kraus, 1995; Lutcavage et al., 1997), southern bluefin tuna (*Thunnus maccoyii*),[1] and other fish species (e.g. Lo et al., 1992). Assessments of juvenile bluefin tuna abundance are considered particularly crucial for effective stock management because these will allow the forecasting of recruitment and long-term population trends (Polacheck et al., 1996; Sissenwine et al., 1998). There is, however, a need to establish the probability of detecting schools and estimating school size before aerial survey data can provide robust population assessments. This need is present regardless of whether the census techniques are simple photography (Lutcavage and Kraus, 1995; Lutcavage et al., 1997) or new laser-based digital remote sensing techniques (Oliver et al., 1994; Lo et al., 1999). As with traditional CPUE-based abundance estimates, knowledge of the effects of oceanographic conditions on depth distribution, surfacing frequency, travel speeds, and residence patterns is critical because these conditions will affect vulnerability to "capture," either on photographic film or as digital data.

To obtain the necessary data, we undertook a study of the horizontal and vertical movements of juvenile Atlantic bluefin tuna using depth sensitive ultrasonic telemetry devices. Ultrasonic telemetry is a proven technique for acquiring the required precise and detailed data on the behaviors of pelagic fishes in relation to oceanographic conditions (e.g. Holland et al., 1990; Dagorn et al., 1999, 2000a; Lutcavage et al., 2000). Besides being useful for improving stock assessments (Brill and Lutcavage, 2001), the resultant data can also help clarify basic ecological relationships and provide inferences on physiological abilities and species-specific behaviors (Carey, 1983; Brill, 1994; Brill et al., 1999).

Materials and methods

Fishing operations were conducted from a 16-m commercial fishing boat (FV *Grumpy*) in the western North Atlantic off the eastern shore of Virginia (Fig. 1A) during June and July 1998. Bluefin tuna were captured with standard recreational trolling gear. The fish were brought aboard with a plastic sling and detached from hooks. Straight line fork length was measured, and a Vemco (Halifax, Nova Scotia, Canada) ultrasonic transmitter (model V32) was attached near the second dorsal fin with nylon straps as described by Holland et al. (1986, 1990). The transmitted signal was detected with a Vemco VR-60 ultrasonic receiver connected to a directional hydrophone mounted on the end of an aluminum pipe. The pipe was clamped to the side of the vessel with a custom designed aluminum bracket that allowed the hydrophone to be rotated to find the relative bearing to the transmitter. Fish depth, encoded by the interval of the transmitter's pulsed signal, was decoded by the receiver and the resultant digital data recorded by an attached laptop computer. Geographic

[1] Cowling, A., C. Millar, and T. Polacheck. 1996. Data analysis of the aerial surveys (1991–1997) for juvenile southern bluefin tuna in the Great Australian Bight. Rep. RMWS/96/4, 87 p. Recruitment Monitoring Program, CSIRO Division of Marine Research, GPO Box 1538, Hobart 7001, Australia.

Table 1

Summary of tracks of five juvenile Atlantic bluefin tuna (*Thunnus thynnus*) equipped with ultrasonic depth sensitive transmitters. Body masses were calculated from fork lengths with the weight-length regression equation provided by Coull et al. (1989).

Fish no.	Fork length cm	Body mass kg	Dates of track (1988)	Duration of track h	Total distance covered km (nmi)	Distance between start and end points km (nmi)	Mean (± SEM) swimming speed knots
1	74	6.7	17–19 Jun	47.2	217 (117)	52.7 (28.4)	2.8 ±0.03
2	91	12.1	23–25 Jun	47.8	267 (144)	11.4 (6.1)	3.0 ±0.03
3	79	8.0	2–3 Jul	30.0	152 (82)	7.7 (4.1)	2.7 ±0.04
4	99	15.4	6–7 Jul	31.2	192 (104)	14.7 (7.9)	3.3 ±0.03
5	106	18.8	10–12 Jul	47.9	289 (156)	32.2 (17.4)	3.2 ±0.03

positions were obtained by using a GPS satellite receiver and were recorded on a second laptop computer every minute. The tracking vessel's position was assumed to be the same as that of the fish. Sea surface temperature and bottom depth were recorded manually every 15 minutes by using a hull-mounted electronic temperature sensor and color fathometer, respectively. Depth-temperature profiles were taken approximately every four hours with a Sippican (Marion, MA) portable XBT system (model MK12).

Aggregate time-at-depth and time-at-temperature distributions were calculated from10-m and 1°C bins (respectively), as described by Holland et al. (1990). These data were subsequently expressed as a fraction of the total time each fish was followed, and the fractional data bins were averaged across all fish. Speed over ground (henceforth referred to simply as "speed") was calculated by assuming that the fish moved in a straight line between successive geographic locations.

Sea surface temperature (SST) data were recorded by the advanced very high resolution radiometer (AVHRR) carried onboard the NOAA-14 polar orbiting operational environmental satellite. High resolution picture transmission (HRPT) data were obtained from the National Coast Watch Active Access System at the National Oceanographic Data Center and had a spatial resolution of 1.25 × 1.25 km pixels. Ocean color data were recorded by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) carried onboard the Orbview-2 spacecraft (Orbimage, Inc., Dulles, VA). The level-2 global area coverage (GAC) data were obtained from the NASA Goddard Space Flight Center's Distributed Active Archive Center. These 4-km resolution data sets included chlorophyll-*a* surface concentration and the diffuse attenuation coefficient at 490 nmi, *in vacuo*. We calculated the occupancy of waters with specific chlorophyll-*a* concentrations and light attenuations from values corresponding to and coincident with the tracks of fishes derived from satellite images. These data were subsequently expressed as a fraction of the total number of observations for each fish, and the fractional data bins were averaged across all fish. For illustrative purposes, we also generated composite images using data from the 21-day period over which all tracking operations were conduced.

Results

The bottom topography in the areas where the fish were tracked is generally featureless, except for small areas where the vertical relief is approximately 2 m above the surroundings. Local fishermen have named these features (Fig.1B and subsequent figures), and the names used in this study are taken from local fishing charts.

Size of fish, starting and ending dates of tracks, duration of tracks, distances covered, distance between starting and ending points, and mean (±SEM) swimming speed of fish are listed in Table 1. With the exception of fish number 4 (referred to simply as "fish 4"), individuals tended to follow highly irregular courses that often repeatedly covered the same areas (Fig. 1B). The mean distance between starting and ending points for all fish was only 11% (range: 4–25%) of the total distance covered (Table 1). From tracking studies of yellowfin tuna (*Thunnus albacares*) in the Pacific, Dagorn et al. (2000a) concluded that such frequent directional changes might be characteristic of foraging behavior. The frequency of observed swimming speeds is shown in Figure 2. Although all fish reached maximum speeds of ≈7 knots for brief periods, over 90% of the observed speeds were less than 3.6 knots.

Horizontal movements

Fish 1 was captured and released at 1340 h, approximately 1.8 km (1 nmi) west of the "26 Mile Hill" (Fig. 3). It proceeded on a southerly course for about 33 h, a direction that carried it over the "Hot Dog" and "Southeast Lumps." After sunset on the second day, the fish reversed its course and eventually recrossed both features. The fish was approximately 5.6 km (3 nmi) south of the "Southeast Lumps," and moving south, when the track was terminated at 1300 h.

Fish 2 was captured approximately 5.6 km (3 nmi) south of the "Southeast Lumps" (Fig. 3) at 1547 h, adjacent to where the track of fish1 was completed four days earlier. It

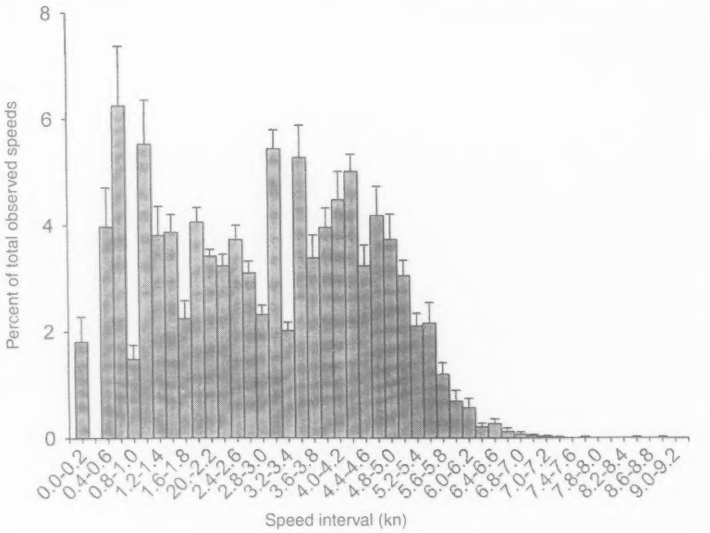

Figure 2

Frequency histogram (mean ±SEM) of observed speed over ground of bluefin tuna. The frequency of each speed interval was calculated as a fraction of the total number of observations for each fish, and speed intervals where then averaged across fish.

proceeded south, then briefly west just before dusk. After dark it turned to the northeast, and then assumed a parallel course to the southwest. From 1000 h on the second day until the end of the track, the fish repeatedly crisscrossed an area approximately 18 km (10 nmi) southeast of the "Southeast Lumps." The fish made one brief excursion during the second day but generally remained in this area until the track was terminated at 1545 h.

Fish 3 was captured and released at 1140 h approximately 11 km (6 nmi) northeast of the "21 Mile Hill" (Fig. 4). It proceeded to the northwest for approximately 4 hours, then turned and retraced its course returning to the point where it was captured approximately 6 hours earlier. This general pattern was repeated for the remainder of the track. Fish 3 favored an area approximately 11 km (6 nmi) northeast of the "21 Mile Hill," although it moved briefly away from this area during the first night and second day.

Fish 4 was captured and released at 1300 h in the same area (northeast of the "21 Mile Hill") as fish 3 (Fig. 4). Its behavior differed significantly from all the other fish in that it swam two relatively straight courses. The first was to the southeast (from the time of release until sunrise the following day) and the second to the northwest (from sunrise until the track ended at 2015 h). (The track had to be abandoned after approximately 31 h when the fish moved into an active U.S. Navy missile test area.) It was also the only individual that moved offshore of the continental shelf.

Fish 5 was captured and released at 1330 h immediately adjacent to the "21 Mile Hill" (Fig. 3). During the first day, the first night, and the morning of the second day the fish stayed either over or adjacent to the "21 Mile Hill" and "26 Mile Hill." It eventually followed a relatively straight course to an area approximately 5.5 km (3 nmi) northeast of the "Fish Hook," were it remained until the track was terminated after 48 hours.

Vertical movements

The vertical movements of the four fish that remained on the continental shelf are shown in Figure 5. Juvenile bluefin tuna made use of the entire water column and undertook frequent, albeit brief, forays to the bottom. Fish 4 showed similar behavior but reached maximum depths of approximately 160 m when its course carried it eastward of the continental shelf (Fig. 6). No abrupt vertical movements were apparent at dawn and dusk, as have been observed in adult Atlantic bluefin tuna (Lutcavage et al., 2000) and juvenile Pacific bluefin tuna (*Thunnus orientalis*) (Marcinek et al., 2001). Similarly, there were no dramatic and unambiguous differences in daytime and nighttime vertical movement patterns (Figs. 5 and 6), as has been observed with bigeye tuna (*Thunnus obesus*) (Holland et al., 1990; Dagorn et al., 1999).

Figure 7 presents the mean (±SEM) time spent at specific depths and at specific temperatures. Juvenile bluefin tuna spent ≈90% of the time at depths less than 15 m, but less than 20% of the time at depths above 3 m. There were no clear differences in daytime and nighttime depth distri-

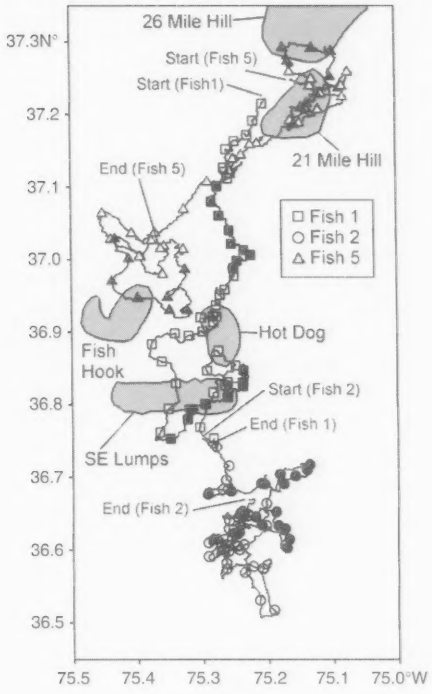

Figure 3

Movements of fish 1, 2, and 5. Symbols represent hourly intervals: open symbols indicate daytime and solid symbols, nighttime.

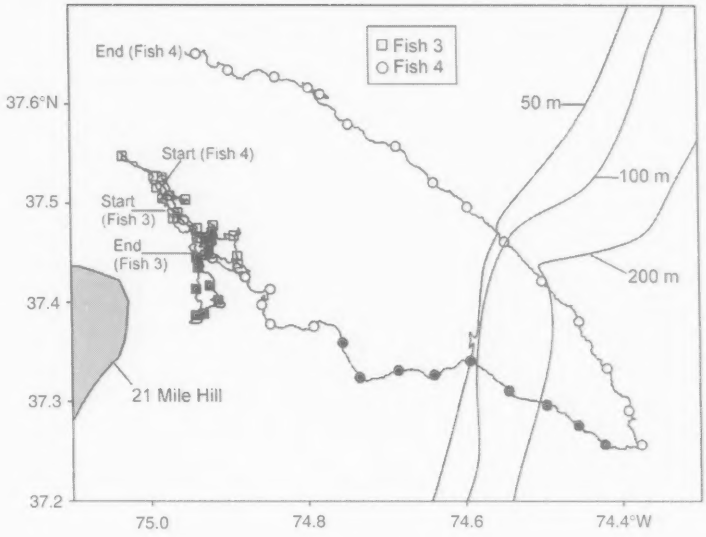

Figure 4

Movements of fish 3 and 4. Symbols represent hourly intervals: open symbols indicate daytime and solid symbols, nighttime. The edge of the continental shelf is shown by the 50, 100-, and 200-m isobath lines.

butions. Although they encountered water temperatures of ≈10°C during their brief descents, fish spent ≈90% of the time in water greater than 20°C and ≈50% of the time in water greater than 24°C.

Occupancy of specific water masses

Figure 8 shows fish movements and sea surface temperatures (SST). Note that specific water masses (except for the Gulf Stream, a portion of which is clearly visible to the southeast) appear ill-defined by SST (Fig. 8). (During the 21-day study period, there was no evidence that an instability in the Gulf Stream resulted in discharge of warm, high-salinity water onto the Virginia continental shelf, as has been occasionally observed [Churchill et al., 1993].)

Figure 9 presents fish movements and chlorophyll-*a* concentrations (i.e. phytoplankton abundance) and water clarity measured as the diffuse attenuation coefficient (1/m) at an *in vacuo* wavelength of 490 nmi (a low diffuse attenuation coefficient indicates high water clarity). Note that, in contrast to sea surface temperature data (Fig. 8), the turbid, plankton-rich water leaving Chesapeake Bay (the "Chesapeake Bay plume") is clearly visible. The Chesapeake Bay plume flows to the south and remains trapped inshore because of the Coriolis effect (Reiss and McConaugha 1999), which is to the right in the Northern Hemisphere. Also visible is the clear oligotrophic mid-Atlantic slope water eastward of the continental shelf.[2] With the exception of fish 4, which made a brief excursion into the mid-Atlantic slope water east of the continental shelf, fish remained in the mid-Atlantic shelf water (i.e. between the extremes of water clarity and phytoplankton abundance immediately to the east and west) (Fig. 9).

Figure 10 presents the frequency histograms for the specific chlorophyll-*a* concentrations and diffuse attenuation coefficients of water occupied by juvenile bluefin tuna. These data confirm that juvenile bluefin tuna restricted their movements primarily to waters with a relatively narrow range of clarity and phytoplankton abundance.

Discussion

Although juvenile bluefin tuna remained within relatively restricted geographical ranges while being tracked (Table 1, Fig. 1), none of these fish showed the repetitive daily behaviors often demonstrated by yellowfin tuna and

[2] Wright, W. R. 1976. Physical oceanography. *In* A summary of environmental information on the continental slope Canadian/United States border to Cape Hatteras, N.C., p. 4-1–4-109. Prepared by TRICOM, The Research Institute of the Gulf of Maine, South Portland, MA, for the Bureau of Land Management, Marine Minerals Division. [Available from National Technical Information Service, U. S. Department of Commerce, Springfield, VA 22161.]

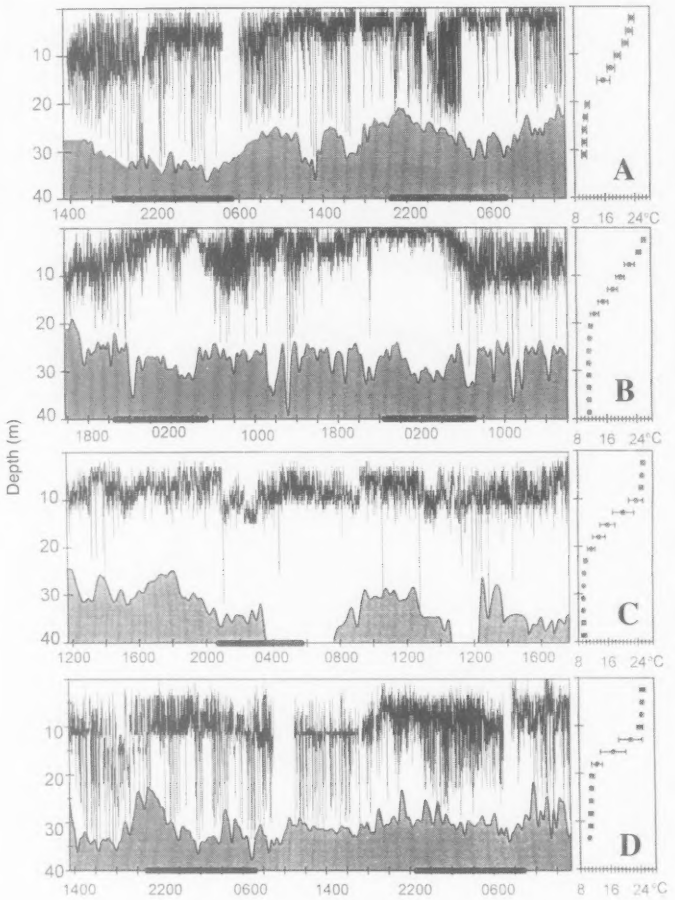

Figure 5

Vertical movements of four juvenile bluefin tuna: (**A**) = fish 1, (**B**) = fish 2, (**C**) = fish 3, (**D**) = fish 5). Bottom topography is shown by the shaded area, and the thick horizontal solid bars indicate nighttime. Depth-temperature profiles (mean ±SEM), recorded during each track by using an expendable bathythermograph (XBT) system, are shown to the right of each vertical movement plot.

skipjack tuna (*Katsuwonus pelamis*). In the Pacific, the latter two species often spend daylight hours associated with reef drop-offs, banks, or man-made fish aggregating devices (FADs), repeatedly move up to ≈5 nmi away at night, then return to the same area the following day (Yuen, 1970; Holland et al., 1990; Marsac and Cayré, 1998; Dagorn et al., 2000a). The continental shelf where the juvenile bluefin tuna were followed is, however, relatively flat compared with the steep topography around the oceanic islands, where many of the yellowfin and skipjack tuna were followed. Unlike the situation in the Pacific, the small topographic features on the mid-Atlantic continental shelf probably do not possess sufficient magnetic signatures that could be detected by the fish (Walker, 1984; Klimley, 1993). Moreover, the movements of the juvenile that we observed closely resembled those of bluefin tuna tracked in the eastern Pacific when they were not near the coast or any apparent significant geological features (Marcinek et al., 2001)

Juvenile bluefin tuna clearly use the entire water column and frequently interact with the bottom when over the continental shelf. Similar behaviors were observed in adult bluefin tuna in the Gulf of Maine (western North Atlantic) (Lutcavage et al., 2000). Frequent vertical movements of juvenile bluefin tuna likely reflect feeding behaviors for capturing sand lance (*Ammodytes* spp.), which

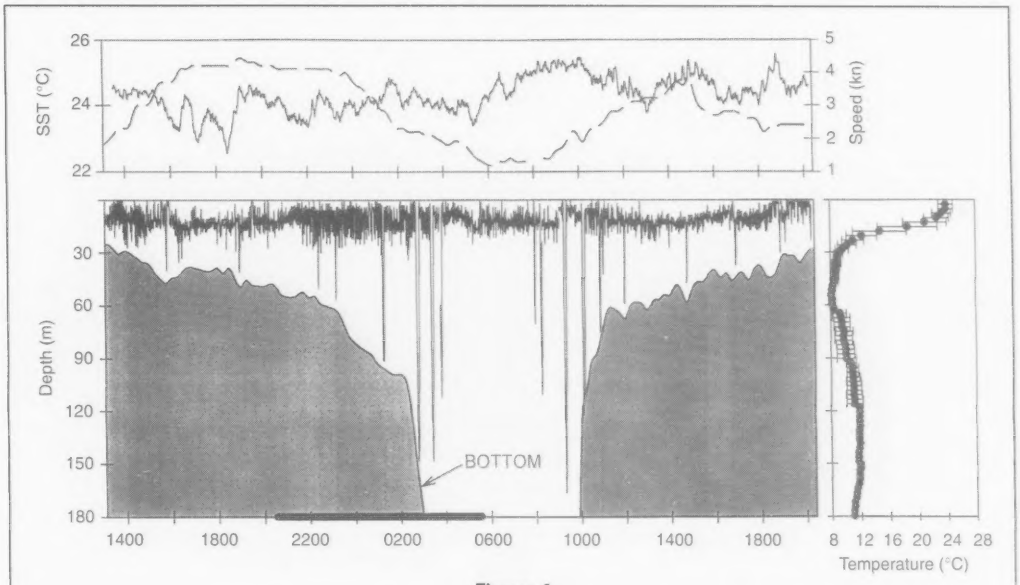

Figure 6

Swimming speed (solid line, upper panel) and vertical movements (lower panel) of fish 4. The change in temperature in the horizontal direction (expressed as sea surface temperature, SST) is shown by the broken line in the upper panel (Brill and Lutcavage, 2001). As in Figure 5, the change in temperature in the vertical direction (mean ±SEM) is shown to the right of the vertical movement plot. Note that changes in swimming speed are not correlated with changes in SST, and that the steepest temperature change the fish could experience moving horizontally (generally less then 0.5°C/km) is several orders of magnitude less then that experienced moving vertically (≈0.6°C/m).

occur throughout the water column during daylight, are abundant in the areas where we tracked the fish, and dominate the diet of tunas in this area (Mason, 1976; Eggleston and Bochenek, 1989). The nature of fish 4's descents up to ≈160 m while off the continental shelf (Fig. 6) remain unclear, although they too may be related to foraging (Dagorn et al., 2000a, 2000b). Their brevity is most likely due to the inability of Atlantic bluefin tuna to withstand temperatures below 10°C for long periods of time, rather than to an intolerance of low ambient oxygen conditions. Although no depth-oxygen profiles were obtained during our study, available data[2] suggest that juvenile tuna did not encounter ambient oxygen levels that were likely to be stressful (Bushnell and Brill, 1991, 1992).

The behavior pattern we observed of short oscillatory dives near the surface is similar to that of both juvenile bluefin tuna in the eastern Pacific (Marcinek et al., 2001) and adult bluefin tuna tracked in the Gulf of Maine (Lutcavage et al., 2000). In all cases, fish spent the majority of their time in the surface layer, although in the Gulf of Maine and eastern Pacific, the temperature of the warmest water available was lower (≈13–22°C) and more variable. As shown in Figure 11, when expressed as the relative change in temperature with depth (i.e. in relation to the surface water temperature occurring during each track), time-at-temperature distributions of juvenile and adult Atlantic bluefin tuna become essentially identical. Moreover, the limiting effects of temperature change on vertical movements are independent of body size. Similarly, yellowfin tuna tracked near the main Hawaiian Islands and off the coast of California occupy the warmest water available, regardless of body size, even though surface water temperature in the two areas differs by more than 5°C (Holland et al., 1990; Block et al., 1997; Brill et al., 1999). Atlantic bluefin tuna, however, are more eurythermal than yellowfin tuna. The latter will rarely expose themselves to more than an 8°C change in temperature, whereas the former regularly subject themselves to a temperature change of up to 13°C (Fig. 11). Surprisingly, the behavior of juvenile bluefin tuna observed by Marcinek et al., (2001) was more like that of yellowfin tuna in that these juvniles would not expose themselves to more then an 8°C temperature change.

It still remains to be conclusively demonstrated, however, whether the vertical movement patterns of tunas and other large pelagic fishes are (as suggested by Brill et al., 1993, 1999) limited by the effects of ambient temperature on cardiac function. Or whether, as suggested by Marcinek et al. (2001), that depth distributions "... may have more to do with the location of prey, and the physiological limitations of the prey, than physiological limitations of the bluefin [tuna]." Moreover, months-long observations

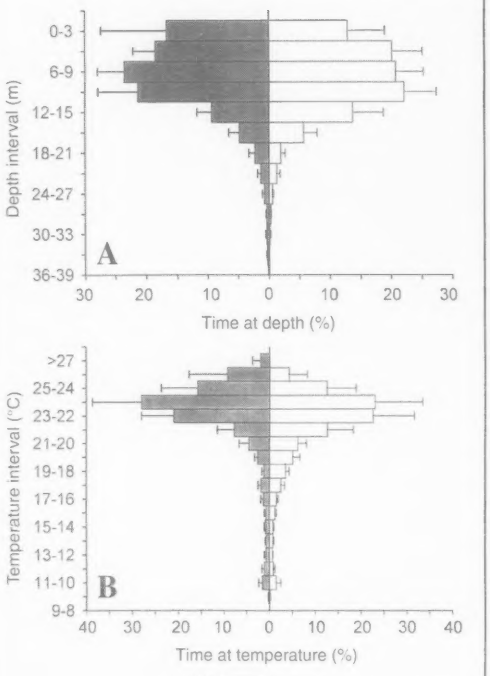

Figure 7

Vertical distribution of five juvenile bluefin tuna expressed as percent time (mean ±SEM) spent at specific depths (**A**) and at specific temperatures (**B**). Shaded bars indicate nighttime and open bars indicate daytime.

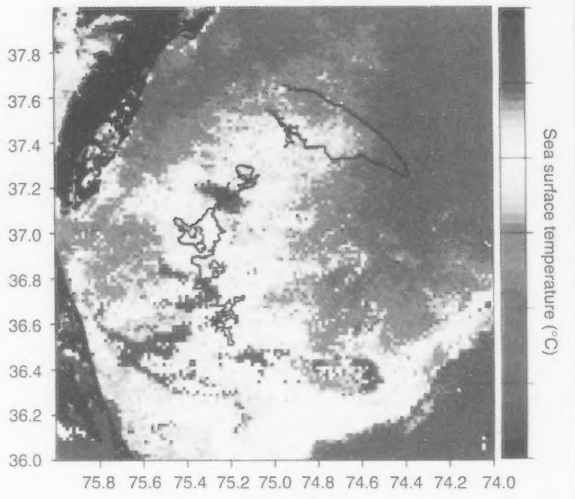

Figure 8

Composite satellite sea surface temperature image (17 June–10 July 1998) and movements of the five juvenile bluefin tuna (Brill and Lutcavage, 2001). Figure reprinted with permission of American Fisheries Society.

of juvenile bluefin tuna in the western Pacific recently obtained with archival (i.e. electronic data recording) tags have shown that the vertical movements of juvenile bluefin tuna can have strong seasonal and geographic components (Kitagawa et al., 2000). In areas and at times (e.g. winter) when there was a strong thermocline, bluefin tuna remained in the uniform-temperature surface layer and demonstrated vertical movement behaviors similar to those observed during the short-term ultrasonic telemetry studies. In the summer, when the themocline was less pronounced, the fish showed very distinct diel periodicity in their vertical movement patterns. They would remain at the surface at night and make rapid vertical movements (from surface to ≈120 m and from ≈21°C to 14°C) during the day. Kitagawa et al. (2000) concluded that the differences in behavior patterns were related to foraging. It is also still an open question as to what extent bluefin tuna's ability to conserve metabolic heat and maintain elevated muscle temperatures (Carey and Teal, 1966) enhances vertical mobility.

Roffer (1987) was apparently the first to propose that movements and abundance of juvenile Atlantic bluefin tuna are controlled by the depth and thickness of the 18.5–20.5°C "preferred habitat" temperature layer. Likewise, Inagake et al. (2001), using archival tags implanted into juvenile bluefin tuna in the western Pacific, found evidence that this temperature range is indeed always "preferred." During the periods of our observations, juvenile bluefin tuna spent the majority of their time (≈80%) in water greater then 22°C. A plausible explanation is that under the conditions of our observation period, juvenile bluefin tuna simply occupy the warmest water available, although a relatively uniform temperature surface layer was evident only during tracks of fish 3, 4, and 5. We also did not find any conclusive indication that juvenile bluefin tuna avoided surface water temperatures above 26°C. Although fish spent less than 20% of time at these temperatures (Fig. 7), less than 20% of the recorded sea surface temperatures (i.e. the warmest water available) were above 26°C.

We also found no relationship between sea surface temperature and horizontal movements (Figs. 6 and 8), although this relationship has been demonstrated for other tuna species in other areas (e.g. Laurs et al., 1977; Fiedler and Bernard, 1987; Uda, 1973). We argue that our results are due to the differences in the vertical and horizontal temperature gradients occurring along the Virginia coast. Juvenile bluefin tuna routinely traveled through the thermocline, moving from the relatively warm surface layer into the mid-Atlantic cold-pool water (Houghton et al., 1982; Houghton and Marra, 1983) underlying it. The fish thus experienced temperature gradients of up to ≈0.6°C/m (Figs. 5 and 6). In contrast, the steepest horizontal temperature gradient in the area where the fish were tracked was approximately three orders of magnitude smaller (≈0.5°C/km). In other words, the frequent vertical movements of juvenile bluefin tuna probably prevent them from detecting and responding to SST gradients.

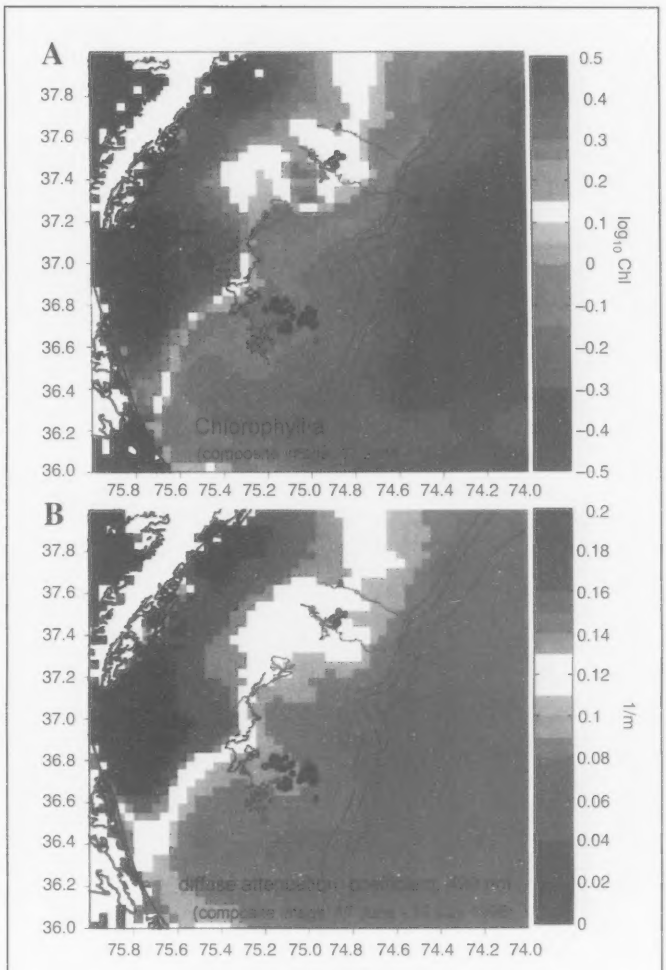

Figure 9

Composite satellite images (17 June–10 July 1998) showing (**A**) chlorophyll-*a* concentrations (mg/m^3) and (**B**) water clarity measured as the diffuse attenuation coefficient (1/m, at an *in vacuo* wavelength of 490 nmi) and movements of the five juvenile bluefin tuna. Locations of juvenile bluefin tuna schools recorded during aerial surveys conducted in 1997 are shown by filled circles. (Lutcavage, M. 1998. Aerial survey of school bluefin tuna off the Virginia Coast, July 1997. Report to the National Marine Fisheries Service, cooperative agreement NA77fm0533. [Available from the author, Edgerton research Laboratory, New England Aquarium, Central Wharf, Boston, MA 02110].) are shown by filled circles. The edge of the continental shelf is indicated by the 50-, 100-, and 200-m isobath lines (Brill and Lutcavage, 2001). Figure reprinted with permission of American Fisheries Society.

Carey (1992) was one of the first to appreciate the importance of vertical thermal structuring and stated "Temperature gradients of 15° to 20°C are not uncommon within the depth ranges of pelagic fish. By moving a few hundred meters vertically, an animal may encounter a greater temperature change than it experiences seasonally or in moving thousands of miles horizontally." As with bluefin tuna, the vertical movements of yellowfin tuna and swordfish also result in their experiencing vertical temperature gradients orders of magnitude greater than horizontal temperature gradients (Carey and Robison, 1981; Carey, 1990; Holland et al., 1990; Cayré and Marsac, 1993). The inabil-

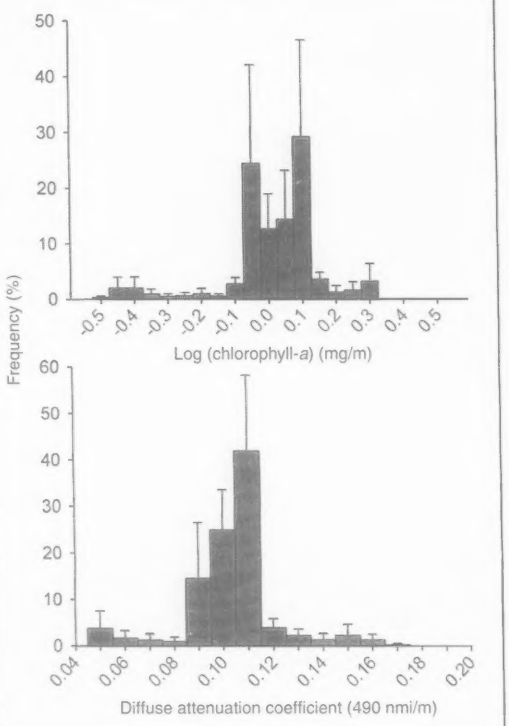

Figure 10

Frequency histogram (mean ±SEM) of chlorophyll-*a* concentrations (mg/m^3) and water clarity measured as the diffuse attenuation coefficient (1/m, at an *in vacuo* wavelength of 490 nmi) in waters along the track lines of five juvenile bluefin tuna (Brill and Lutcavage, 2001). The span of the horizontal axes show the approximate range of these variables present off the eastern shore of Virginia.

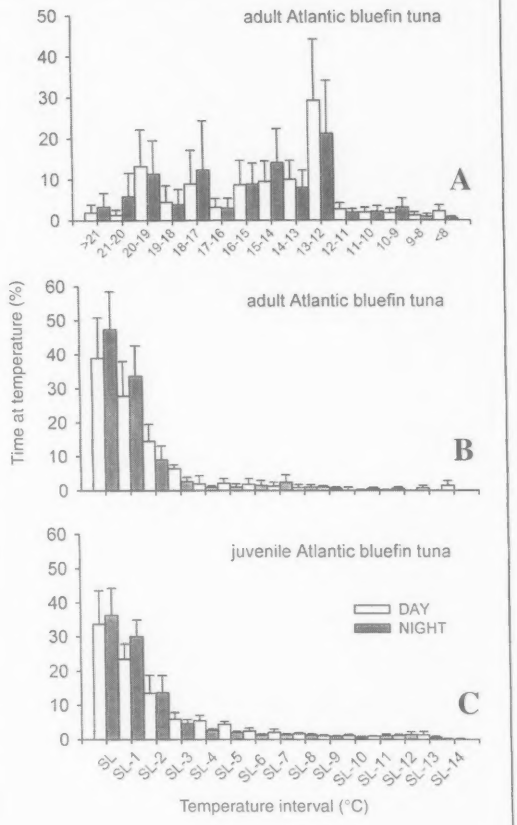

Figure 11

Frequency histograms (mean ±SEM) showing time spent at specific temperatures by adult bluefin tuna tracked in the Gulf of Maine (western North Atlantic) with temperatures expressed as water temperature (**A**), and with temperatures expressed in relation to surface layer temperature (**B**), data taken from Lutcavage et al., 2000). Equivalent data for juvenile bluefin tuna are presented in panel **C**. Shaded bars indicate nighttime and open bars indicate daytime.

ity of fish to sense shallow horizontal temperature gradients in the face of the steep vertical temperature gradients they routinely experience may explain, therefore, why Power and May (1991) and Podestá et al. (1993) could find no correlation between SST "fronts" and the apparent abundance of yellowfin tuna in the Gulf of Mexico and swordfish in the western north Atlantic.

In contrast to SST, water clarity and phytoplankton abundance appear to have a strong influence on the horizontal movements of juvenile bluefin tuna (Figs. 9 and 10). Tunas are sight hunters, and possess the highest visual acuity of any teleost (Nakamura, 1968). We suspect that juvenile bluefin tuna remain in water masses with a standing phytoplankton biomass sufficient to support concentrations of prey, but where turbidity is low enough that visual prey detection and prey capture abilities are not impeded. Our conclusion is further supported by the locations of juvenile bluefin tuna schools detected in aerial surveys conducted in 1997.[3] Although satellite data showing diffuse attenuation coefficients and chlorophyll-*a* concentrations are not available for 1997, bluefin tuna schools were located in the areas where the fish carrying ultrasonic transmitters remained (Fig. 9). Olson and Podestá (1987), Olson et al. (1994), and Humston et al. (2000) have also concluded that aggregations of highly mobile species

[3] Lutcavage, M. 1998. Aerial survey of school bluefin tuna off the Virginia Coast, July 1997. Report to the National Marine Fisheries Service (cooperative agreement NA77FM0533). [Available from the author, Edgerton Research Laboratory, New England Aquarium, Central Wharf, Boston, MA 02110.]

at fronts result from cues other than SST, such as changes in the photic environment associated with phytoplankton distribution, changes in prey abundance, or enhanced forage opportunities.

Aerial survey techniques and population assessments of juvenile bluefin tuna

Techniques for interpretation of aerial survey data with respect to population assessments are complex (e.g. Lo et al., 1999; Newlands and Lutcavage, 2001), and a thorough discussion is beyond the scope of our present study. We can, however, use our data on juvenile bluefin tuna's vertical movements and distribution patterns to provide some inferences as to how often they are likely to be visible at the ocean's surface or detectable at a specific depth. Juvenile bluefin tunas spent less than 13% of daylight hours at depths of 0–3 m (Fig. 7), where visual or photographic detection is possible. The depth distribution of juvenile fish was similar to that of adult bluefin tuna tracked in the Gulf of Maine (12% of daylight hours at depths of 0–4 m; Lutcavage et al., 2000). Abundance estimates based solely on photographic data will, therefore, have to be corrected to account for the significant number of fish that maybe be present, but that are beyond detection range. Fish detection systems that use lasers (the so called "light detection and range" or "LIDAR" systems) are expected to have a depth detection zone of up to 60 m (Oliver et al., 1994). This detection zone encompasses almost the entire water column over the sections of continental shelf where juvenile bluefin tuna are likely to be found. Moreover, if the behavior of the fish that moved into deeper water off the continental shelf is assumed typical, then juvenile bluefin tuna would be detected by LIDAR systems even in deep water. The relatively small net displacement distance (i.e. distance between start and end points, Table 1) may require the development of filtering algorithms to reduce errors caused by double counting if parallel transects are flown less than ≈50 km apart, or if the same area is resurveyed weekly or more often. Conversely, significant fish aggregations could be missed if parallel transects are too widely spaced.

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Differences in diet of Atlantic bluefin tuna (*Thunnus thynnus*) at five seasonal feeding grounds on the New England continental shelf*

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Abstract–The stomachs of 819 Atlantic bluefin tuna (*Thunnus thynnus*) sampled from 1988 to 1992 were analyzed to compare dietary differences among five feeding grounds on the New England continental shelf (Jeffreys Ledge, Stellwagen Bank, Cape Cod Bay, Great South Channel, and South of Martha's Vineyard) where a majority of the U.S. Atlantic commercial catch occurs. Spatial variation in prey was expected to be a primary influence on bluefin tuna distribution during seasonal feeding migrations. Sand lance (*Ammodytes spp.*), Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), squid (Cephalopoda), and bluefish (*Pomatomus saltatrix*) were the top prey in terms of frequency of occurrence and percent prey weight for all areas combined. Prey composition was uncorrelated between study areas, with the exception of a significant association between Stellwagen Bank and Great South Channel, where sand lance and Atlantic herring occurred most frequently. Mean stomach-contents biomass varied significantly for all study areas, except for Great South Channel and Cape Cod Bay. Jeffreys Ledge had the highest mean stomach-contents biomass (2.0 kg) among the four Gulf of Maine areas and Cape Cod Bay had the lowest (0.4 kg). Diet at four of the five areas was dominated by one or two small pelagic prey and several other pelagic prey made minor contributions. In contrast, half of the prey species found in the Cape Cod Bay diet were demersal species, including the frequent occurrence of the sessile fig sponge (*Suberites ficus*). Prey size selection was consistent over a wide range of bluefin length. Age 2–4 sand lance and Atlantic herring and age 0–1 squid and Atlantic mackerel were common prey for all sizes of bluefin tuna. This is the first study to compare diet composition of western Atlantic bluefin tuna among discrete feeding grounds during their seasonal migration to the New England continental shelf and to evaluate predator-prey size relationships. Previous studies have not found a common occurrence of demersal species or a predominance of Atlantic herring in the diet of bluefin tuna.

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Atlantic bluefin tuna (*Thunnus thynnus*) are widely distributed throughout the Atlantic Ocean and have attracted valuable commercial and recreational fisheries in the western North Atlantic during the latter half of the twentieth century. The western North Atlantic population is considered overfished by the International Commission for the Conservation of Atlantic Tunas (NMFS, 1999). Bluefin tuna are the largest scombrid species, and the largest teleost occurring in the Gulf of Maine (Bigelow and Schroeder, 1953). Bluefin tuna migrate to coastal waters off New England during warmer months, feeding on local concentrations of prey. This migration supports a major component of the U.S. Atlantic commercial fishery for bluefin tuna; from 1978 to 1992 New England accounted for between 73% and 98% of annual commercial landings (Chase, 1992; and NMFS, 1995). Substantial annual variation has been seen in the harvest locations on the New England continental shelf (Chase, 1992). Spatial variation in prey populations is suspected to be the primary influence on these annual aggregations of bluefin tuna. Adaptations in the circulatory system of the bluefin tuna allow these fish to retain metabolic heat, facilitating the regulation of body temperature (Carey and Teal, 1969) and assisting in the efficient transfer of energy from consumed prey to fast growth rates and large body size. These adaptive features also allow bluefin tuna to make extensive migrations into cold-temperate waters in search of prey. Diet information is necessary to improve the understanding of seasonal movements of bluefin tuna and predator-prey relationships in the New England continental shelf region, and as a baseline for bioenergetic analyses. Information on the feeding habits of this economically valuable species and apex predator in the western North Atlantic Ocean is limited, and nearly absent for the seasonal feeding grounds where most U.S. Atlantic commercial catches occur.

Previous food habit studies have shown that western North Atlantic bluefin tuna are opportunistic feeders on a wide variety of finfish, cephalopods, and crustaceans (Crane, 1936; Krumholz, 1959; Dragovich, 1970; Mason, 1976; Holliday, 1978; Eggleston and Bochenek, 1990; Matthews et al.[1]). Pinkas (1971) reported similar results for Pacific bluefin tuna (*Thunnus thynnus orientalis*). These bluefin tuna food habit studies either reported on small numbers of samples or were qualitative studies on samples distributed over a broad geographic range. Previous studies have not evaluated size relationships between bluefin tuna and their prey and the amount of food consumed. The present study targeted regions of the New England giant tuna (>140 kg) fishery to quantitatively analyze stomach contents of bluefin tuna among discrete seasonal feeding grounds and to investigate predator-prey size relationships for this species in the Gulf of Maine.

* Contribution 3 of the Massachusetts Division of Marine Fisheries, Gloucester, MA 01930.

[1] Matthews, F. D., D. M. Damkaer, L. W. Knapp, and B. B. Collette. 1977. Food of western North Atlantic tunas (*Thunnus*) and lancetfish (*Alepisaurus*). Nat. Oceanic Atmos. Admin. Tech. Rep. NMFS SSRF-706, Washington, D.C., 19 p.

Materials and methods

Study area

Five fishery areas (Jeffreys Ledge, Stellwagen Bank, Cape Cod Bay, Great South Channel, and South of Martha's Vineyard [Fig. 1]) were selected for their traditional association with the bluefin fishery and because geographic and bathymetric differences among areas could result in distinct prey communities. The northernmost area, Jeffreys Ledge, is a major bathymetric feature in the Gulf of Maine and is important for commercial fisheries from northern Massachusetts, New Hampshire, and southern Maine. Stellwagen Bank is a distinct bathymetric ridge located on the eastern boundary of Massachusetts Bay (DOC[2]) that provides close access for ports from Gloucester to Cape Cod. Cape Cod Bay is a large, relatively shallow Gulf of Maine bay that is semi-enclosed on three sides by the land mass of Cape Cod and the south shore of Massachusetts. The two southern areas, Great South Channel and the area south of Martha's Vineyard, are larger regions with less distinct bathymetric features and are separated by Nantucket Shoals. The Great South Channel covers a wide nearshore region running east of Chatham and Nantucket and is bordered by the slopes of Nantucket Shoals on the west. The area south of Martha's Vineyard is located on the continental shelf off southern New England and is distinguished from the other areas by its warmer water, predominance of smaller bluefin tuna (<50 kg), and the seasonal occurrence of other large pelagic fish, such as marlins and tropical tunas.

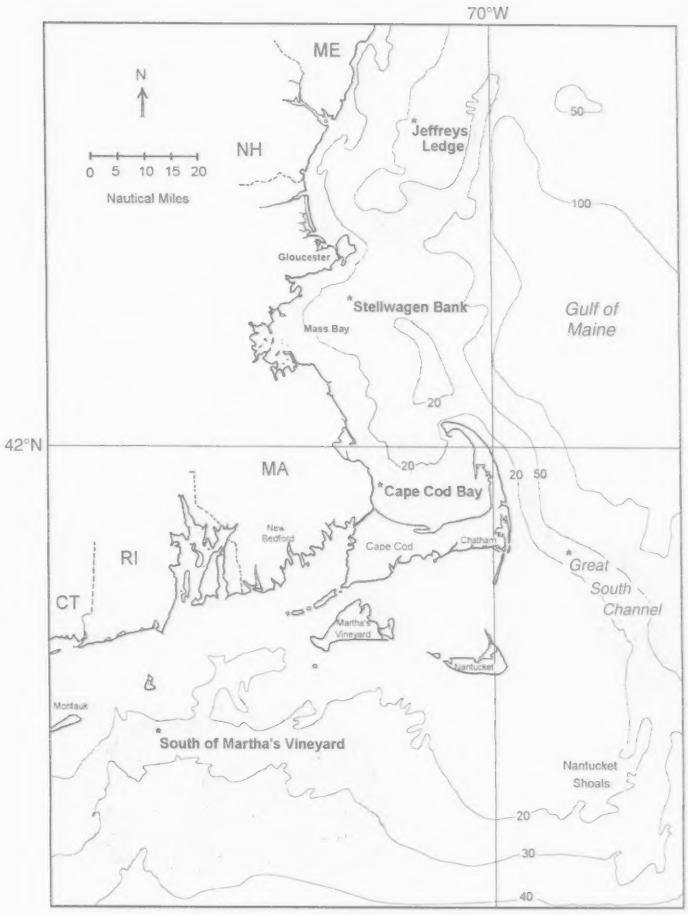

Figure 1

Map of the five bluefin tuna feeding grounds used as study areas (★) July–October 1988–92. Depths are given in fathoms.

Commercial catch records and trawl survey indices of abundance indicate that Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) are the principal pelagic fish species for all these study areas (Clark and Brown, 1976; and NOAA, 1998). Atlantic herring occur in lower relative abundance in the region south of New England than in northern regions. Jeffreys Ledge and Great South Channel are primary spawning locations for Atlantic herring. Catch records and trawl survey indices indicate that the following prey species have been abundant in the study areas: silver hake (*Merluccius bilinearis*), butterfish (*Peprilus triacanthus*), northern shortfin squid (*Illex illecebrosus*), and longfin inshore squid (*Loligo pealeii*).

Sample collection and analysis

Bluefin stomach samples were collected primarily from commercial landings at ports in Massachusetts during the 1988–92 seasons (July–October). Sportfishing tournaments were a secondary source of stomach samples. Handgear landings (rod and reel, handline, and harpoon) were primarily collected in Gloucester and Cape Cod. Purse-seine landings were also a large source of samples, and were collected in Gloucester, New Bedford, and Cape Cod. A majority of stomach samples was collected during 1989 and 1990. A reduced number of samples after 1990 was influenced by the increasing practice of gutting bluefin at sea to sustain a quality product for the sashimi export market.

Most samples were collected at the docks and processing locations of commercial tuna buyers. The vessel captain or tuna buyer was interviewed for location of catch.

[2] DOC (Department of Commerce). 1991. Stellwagen Bank National Marine Sanctuary, Draft environmental impact statement/management plan. U.S. Dep. Commerce (DOC), Nat. Oceanic Atmos. Adm., Sanctuaries and Reserves Division, Washington, D.C., 238 p.

The curved fork length (CFL) and weight of the catch were recorded from the National Marine Fisheries Service (NMFS) tuna logbook. Stomachs were removed by cutting the esophagus above the pylorus and were stored on ice until analysis later that day or were frozen for analysis at a later date. Stomach samples were typically removed from bluefin tuna the day of capture, except those from purse-seine landings, where the catch was often submerged in ice for one or two days prior to landing.

Stomach contents were identified to the lowest possible taxon and weights and counts were made of individual prey species. Wet weights of prey were measured with Homs tubular scales (±5 g) after contents were rinsed through a standard testing sieve (2.00-mm mesh). Prey counts were made only when all individual prey items could be identified and counted for a given stomach sample. Because bluefin tuna consume relatively large prey items and swallow prey whole, species identification was possible for nearly all contents. Skeletal remains were compared with the skeletons of known specimens to assist with identification. Fish contents that could not be identified were categorized as "unidentified fish." Otoliths, squid beaks, and skeletal traces less than 5 g were rounded up to a minimum weight of 5 g.

Stomach-contents data were analyzed by frequency of occurrence, percent composition by number, and percent composition by weight for each prey item (Hyslop 1980; Bowen 1986). Frequency of occurrence can indicate prey composition and availability, and number and weight percentages can represent the quantity a prey item contributes to a diet. "Stomach-contents biomass" refers to all prey in stomach contents, and "prey weight" refers to the weight of individual prey species.

Stomach samples were assigned a status of "empty," "chum," "chum and prey," or "prey only." Chum refers to cut pieces of bait fish that fishermen use to attract bluefin. Both empty and chum stomach samples were eliminated from further data analysis. For "chum and prey" stomachs, chum weight was eliminated from the analysis, and prey weight was included because chum and natural prey were easily distinguished in bluefin tuna stomachs. When the status of contents, or the veracity of catch location could not be resolved, the samples were eliminated from the analysis.

Statistical analysis

Stomach-contents biomass data were analyzed to determine differences among the five fishery areas. Prey weight data were tested for normality (Shapiro and Wilk, 1965) and equality of variance (BMDP, 1990). Stomach-contents biomass data were transformed to natural logarithms and tested for area differences by using the Brown-Forsythe test for unequal variances and the Welch test for pairwise comparisons of areas (BMDP, 1990).

The species composition of stomach contents were tested among areas with the Spearman rank correlation test, under the null hypothesis of no association between species composition and feeding area. The twelve most common prey species were ranked according to frequency of occurrence for each location. The Spearman rank correlation test was applied by pairwise ranking for all locations, excluding missing cases.

Bluefin tuna size was compared with prey length and stomach-contents biomass data by using the Pearson product moment correlation coefficient (Sokal and Rohlf, 1981) to test for significant associations between prey and predator length, and to correlate bluefin tuna weight and stomach-contents biomass for all samples from the Gulf of Maine. The relationship between bluefin tuna size and food consumed was also evaluated by comparing the ratio of stomach-contents biomass and tuna weight (% kg wet weight of prey biomass/kg wet weight of tuna) to tuna length (curved fork length) (Young et al., 1997). The area south of Martha's Vineyard area was excluded from tests on size relationships because of the limited sample numbers of juvenile bluefin tuna collected there.

Results

A total of 819 bluefin tuna stomachs were analyzed during 1988–92 (Table 1) and 568 contained prey; empty stomachs (206) and "chum only" samples (45) were eliminated from further analysis. Approximately equal quantities of the samples with prey came from purse-seine landings (273) and from rod and reel and handline landings (264). The fishing method used for the hook-and-line landings was recorded for 242 samples and was evenly divided between chumming (where chum was used as bait) (123) and trolling (119). Size composition of sampled bluefin tuna was similar for the four Gulf of Maine study areas; a large majority of fish were large, mature adults, estimated to be age 10 and older (Mather and Schuck, 1960). In contrast, nearly all fish sampled from the area south of Martha's Vineyard were small juveniles, ages 2–6. Tuna sampled from Cape Cod Bay had the largest average size (251 cm CFL, and 273 kg).

Prey composition

All areas combined Stomach contents comprised at least 21 species of teleosts, two species of elasmobranchs, and at least nine species of invertebrates (Table 2). Stomach-contents biomass in terms of taxonomic composition was dominated by *Osteichthyes* (Fig. 2A). Of the invertebrates, only squid ("squid" refers to two species, *Loligo pealei* and *Illex illecebrosus*) were a consistent component of prey composition. Although squid accounted for only about 2% of the stomach-contents biomass, it was the second most common prey, occurring in a third of all stomach samples. The only other common invertebrate was the fig sponge (*Suberites ficus*) found in Cape Cod Bay. Despite the large diversity of prey items, few species made major contributions to overall prey composition. Sand lance (*Ammodytes ssp*), squid, Atlantic herring, Atlantic mackerel, and bluefish (*Pomatomus saltatrix*) exceeded all other prey in terms of frequency of occurrence and accounted as a group for 88% of total stomach-contents biomass (Fig. 2B). In the Gulf of Maine areas, sand lance, and Atlantic herring were the major prey in the diet of bluefin tuna during

Table 1

Summary of number of bluefin tuna stomach samples collected at five study areas on the New England continental shelf, July–October 1988–92. Also included are lengths (curved fork length [CFL], cm) and weights (kg) of sampled tuna. "Other" column refers to twelve samples with prey collected at nearshore fishing areas in the Gulf of Maine that were outside the five study areas.

Sample category	Jeffreys Ledge	Stellwagen Bank	Cape Cod Bay	Great South Channel	South of Marths's Vineyard	Other	Total
By year							
1988	13	30	16	0	0	0	59
1989	13	33	28	88	13	1	176
1990	57	15	26	61	33	2	194
1991	34	8	13	34	2	8	99
1992	6	7	26	0	0	1	40
By condition of stomach							
Number with prey	123	93	109	183	48	12	568
Number with chum	19	17	6	0	1	2	45
Number empty	5	1	158	27	8	7	206
Total	147	111	273	210	57	21	819
Mean length of tuna	221	240	251	221	124	221	227
SD	32	35	19	38	30	37	44
Mean weight of tuna	186	243	273	196	36	205	215
SD	78	94	58	90	38	83	97

the study period. Twenty-one bluefin tuna stomach samples were collected outside of the five study areas; mostly at two inshore locations north of Gloucester and south of Stellwagen Bank.

Jeffreys Ledge Atlantic herring were the dominant prey in the 123 stomach samples from Jeffreys Ledge (Table 3). The frequency of occurrence for Atlantic herring (74%) was the second highest and the percentage of stomach-contents biomass (87%) was the highest for any individual prey item among areas. Squid were in nearly half of all samples, but comprised less than 2% of stomach-contents biomass. Atlantic mackerel were the third most common prey for this region (32% occurrence). All other prey species occurred incidentally. Menhaden (*Brevoortia tyrannus*) and pollock (*Pollachius virens*) were unique to samples from Jeffreys Ledge. Mean stomach-contents biomass (~2.0 kg) was the highest among study areas and few empty stomachs were found.

Stellwagen Bank As at Jeffreys Ledge, a single species dominated the stomach-contentss from Stellwagen Bank. Sand lance were found in nearly 80% of 93 stomachs and accounted for nearly 70% of the stomach-contents biomass (Table 3). Atlantic herring, squid, spiny dogfish (*Squalus acanthias*), Atlantic mackerel, and bluefish tuna were secondary prey items, with frequencies of occurrence ranging from 9% to 14%. All other prey species found in stomach contents from Stellwagen Bank occurred incidentally, and there were no species from this area that were unique to the overall study area.

Cape Cod Bay Unlike diet composition for the other study areas, diet composition for Cape Cod Bay did not indicate a dominant pelagic prey but did include the common occurrence of demersal prey. Six prey species were only found in Cape Cod Bay. Squid occurred most frequently but accounted for only 2% of stomach-contents biomass biomass (Table 3). The fig sponge was the top prey in terms of percentage by weight (27%). The diet of bluefin tuna caught in Cape Cod Bay displayed the most diversity among study areas. A total of 16 prey species were identified, of which eight were demersal species. Three species of flounder were identified, representing 9% of the stomach-contents biomass. The occurrence of bluefish tuna as prey in Cape Cod Bay (25%) was the highest among study areas. The amount of food in Cape Cod Bay stomach samples was the lowest for the four Gulf of Maine locations; 60% of the stomachs collected from this area were empty.

Great South Channel A large number of stomach samples with prey (183) were collected from the Great South Channel during 1989–91. The most abundant prey was sand lance, occurring in 62% of the stomach samples and accounting for 28% of the stomach-contents biomass. Atlantic herring was also important, with a frequency of occurrence of 27% and stomach-contents biomass of 48%. As with Stellwagen Bank and Jeffreys Ledge, squid was an important secondary prey item, and bluefish and Atlantic mackerel were secondary prey of lesser importance. Four species were unique to Great South Channel samples: shrimp (*Pandalus* spp.), finger sponge (*Haliclona oculata*), silverstripe halfbeak (*Hyporhamphus unifasciatus*), and Atlantic cod (*Gadus morhua*).

South of Martha's Vineyard Only 48 stomachs with prey were analyzed from the area south of Martha's Vineyard.

Table 2

Stomach contents of bluefin tuna caught off New England during 1988–92. Prey species are combined for all five study areas, including 12 samples from outside of the study areas. Percent frequency of occurrence (% O) and percent weight (% W) data were determined from the 568 stomach samples that contained prey.

Prey species		Frequency of occurrence	Total weight (g)	% O	% W
Sand lance	*Ammodytes* (spp.)	194	128,240	34.2	22.6
Atlantic herring	*Clupea harengus*	167	299,550	29.4	52.8
Atlantic mackerel	*Scomber scombrus*	108	18,930	19.0	3.3
Bluefish	*Pomatomus saltatrix*	55	40,830	9.7	7.2
Butterfish	*Peprilus triacanthus*	21	1685	3.7	0.3
Silver hake	*Merluccius bilinearis*	16	1490	2.8	0.3
Windowpane	*Scopthalmus aquosus*	12	1890	2.1	0.3
Hake	*Urophycis* (spp.)	11	2500	1.9	0.4
Winter flounder	*Pseudopleuronectes americanus*	8	1820	1.4	0.3
Atlantic menhaden	*Brevoortia tyrannus*	7	5500	1.2	1.0
Sea horse	*Hippocampus erectus*	7	40	1.2	<0.05
Atlantic cod	*Gadus morhua*	6	22,840	1.1	4.0
Fourspot flounder	*Paralichthys oblongus*	2	370	0.4	0.1
American plaice	*Hippoglossoides platessoides*	2	310	0.4	0.1
Wrymouth	*Cryptacanthodes masculatus*	2	1300	0.4	0.2
Pollock	*Pollachius virens*	1	940	0.2	0.2
Filefish	*Monocanthus hispidus*	1	30	0.2	<0.05
Halfbeak	*Hyporhamphus unifasciatus*	1	120	0.2	<0.05
Longhorn sculpin	*Myoxocephalus octodecimspinosus*	1	280	0.2	<0.05
Unidentified fish	Teleostei	34	605	6.0	0.1
Spiny dogfish	*Squalus acanthias*	13	10,490	2.3	1.9
Skate	*Raja* (spp.)	13	4670	2.3	0.8
Skate egg case	*Raja* (spp.)	3	20	0.5	<0.05
Squid	Cephalopoda	186	10,835	32.8	1.9
Octopus	Cephalopoda	1	30	0.2	<0.05
Shrimp	*Pandalus* (spp.)	5	25	0.9	<0.05
Lobster	*Homarus americanus*	2	230	0.4	<0.05
Argonaut	*Argonauta argo*	2	25	0.4	<0.05
Crab	*Cancer* (spp.)	2	15	0.4	<0.05
Salp	Salpidae	2	60	0.4	<0.05
Fig sponge	*Suberites ficus*	30	11,510	5.3	2.0
Finger sponge	*Haliclona oculata*	1	50	0.2	<0.05
Stomachs with chum and prey		95	107,430 (chum)		
Stomachs with chum only		45	49,040 (chum)		
Empty stomachs		206	—		
Total stomachs with prey		568	567,230		
Total stomachs sampled		819	723,700		

Giant bluefin were scarce in this area during the study period and numerous samples could not be used because the bluefin tuna were caught in association with trawler fleet discards. This area is distinguished from the others by a predominance of juvenile bluefin tuna . Four prey species were unique to this area: lined sea horse (*Hippocampus erectus*), argonaut (*Argonauta argo*), planehead filefish (*Monocanthus hispidus*), and octopus (Cephalopoda). The filefish and seahorse were associated with bluefin tuna foraging at sargassum weed communities. Squid and Atlantic mackerel were the two most important prey for this area. The frequency of occurrence and percentage of prey weight for mackerel and butterfish were the highest among study areas. Combined stomach-contents biomass for squid, mackerel, and butterfish represented nearly 80% of the stomach contents for this area.

Comparison of study areas The top 12 prey items, overall, were ranked for each area by frequency of occurrence, and area differences were tested with Spearman rank correlation. Of the ten pairwise comparisons, only Stellwagen Bank and Great South Channel showed a significant association in the ranking of prey items (r=0.98, P<0.02), attributable to a high rank of sand lance and a similar ranking of squid, Atlantic herring, and Atlantic mackerel for both areas.

Stomach-contents biomass

Comparison of study areas Large differences in stomach-contents biomass were found: Jeffreys Ledge averaged nearly 2 kg, followed by approximately 1 kg for Stellwagen Bank and Great South Channel, and less than 0.5 kg for the remaining areas. Stomach-contents biomass data from the five areas were positively skewed and heteroscedastic. The natural logarithm-transformed data for Stellwagen Bank, Cape Cod Bay, and Great South Channel were normal (Wilk-Shapiro test, P>0.05). Transformed biomass data for the other two areas still differed significantly from normality. Transformation of biomass data reduced the inequality of variances, but significant differences (Levene's test, P<0.05) remained, which precluded use of analysis of variance. The Brown-Forsythe test for unequal variances showed a significant effect of area on stomach-contents biomass (P<0.0001). Pairwise comparisons of the equality of prey weight means were made with the Welch test (Bonferroni corrected significance level of P=0.005). All area pairwise comparisons of stomach-contents biomass were significantly different except that between Cape Cod Bay and Great South Channel (P=0.816).

The similarity in the amount of food found at Cape Cod Bay and Great South Channel was also indicated by the geometric mean of stomach-contents biomass (Table 4). The arithmetic mean of stomach-contents biomass was higher at the Great South Channel than Cape Cod Bay, but this value was biased by a few samples with large amounts of prey. The stomach-contents biomass range for Cape Cod Bay did not exceed 3.0 kg, in contrast to the wider range for the Great South Channel up to 16.0 kg, including 13 samples over 3.0 kg. The use geometric means reduced the bias of skewness and indicated that samples from Jeffreys Ledge contained the most prey and that the amounts declined moving southward.

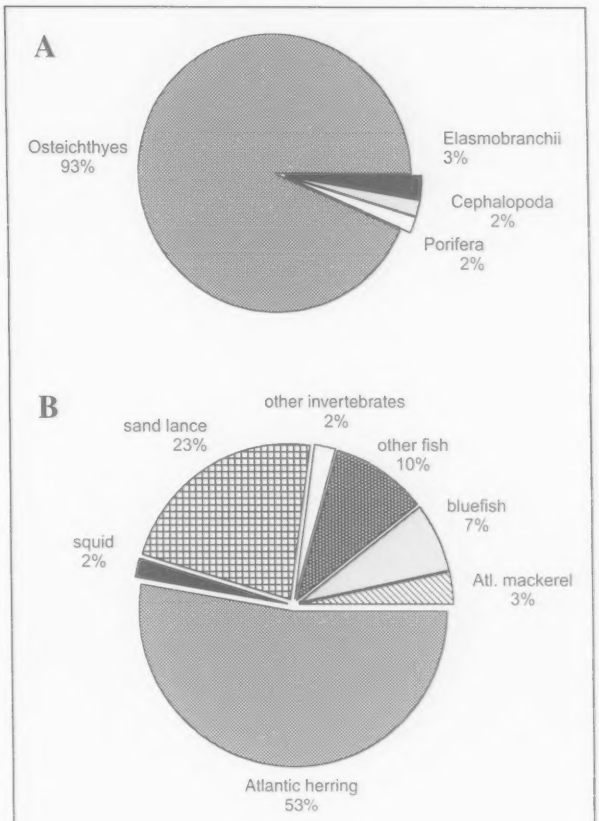

Figure 2

Percent prey weight composition in stomach contents of bluefin tuna caught off New England during 1988–92 (n=568). The taxonomic composition (**A**) includes 0.05% Crustacea and 0.01% Urochordata. The comparison by major prey type (**B**) comprises the five most common prey and all remaining fish and invertebrates.

Effect of tuna size Increased stomach-contents biomass with increasing body size (due to increasing gape and stomach size) was not clearly demonstrated from these data. Correlation of stomach-contents biomass to bluefin weight was not significant for Gulf of Maine samples. A scatterplot of data for the Gulf of Maine samples revealed that a large majority of the samples contained small amounts of food, regardless of body size (Fig. 3). A size-related trend was observed in that only very large bluefin tuna (>250 kg) contained more that 6 kg of food. Size effects were also compared by using the ratio of stomach-contents biomass and tuna weight (% kg/kg, wet weight) to tuna length. The percentage of food to body mass declined with increasing bluefin tuna length (Fig. 4). Food observed in 120–149 cm bluefin tuna averaged over 1% of their body weight, and declined to approximately 0.5% for bluefin tuna over 230 cm. The high ratios primarily resulted from large meals of Atlantic herring or sand lance. Cape Cod Bay ratios were consistently the lowest among the four areas, ranging from 0.1 to 0.2%.

Characteristics of prey species

Prey size Prey size was evaluated for 190 stomach samples that contained measurable prey from the four Gulf of Maine areas. A total of 1866 prey items were measured, of which 95% were either sand lance, Atlantic herring, squid, or Atlantic mackerel (Table 5). A significant positive cor-

Table 3

Stomach contents of bluefin tuna caught off New England during 1988-1992, listed by the five study areas. Percent frequency of occurrence (% O) and percent by weight (% W) were calculated for each prey species.

	Jeffreys Ledge		Stellwagen Bank		Cape Cod Bay		Great South Channel		South of Martha's Vineyard	
Prey species	% O	% W	% O	% W	% O	% W	% O	% W	% O	% W
Sand lance	3.3	1.8	79.6	69.3	0	0	62.3	28.3	0	0
Atlantic herring	74.0	87.2	14.0	6.0	8.3	3.1	27.3	48.4	2.1	2.5
Atlantic mackerel	31.7	2.0	10.8	2.6	18.3	12.7	8.2	0.6	33.3	56.2
Bluefish	7.3	3.5	8.6	17.5	24.8	14.7	4.9	5.7	0	0
Butterfish	2.4	<0.05	1.1	<0.05	5.5	1.5	1.6	0.2	16.7	10.4
Silver hake	3.3	0.2	0	0	0	0	2.2	0.3	10.4	2.9
Windowpane	0	0	0	0	10.1	4.1	0	0	0	0
Hake	4.1	0.7	1.1	0.2	0.9	0.2	0	0	8.3	9.9
Winter flounder	0	0	0	0	6.4	3.9	0	0	0	0
Atlantic menhaden	5.7	2.3	0	0	0	0	0	0	0	0
Sea horse	0	0	0	0	0	0	0	0	14.6	0.7
Atlantic cod	0	0	0	0	0	0	3.3	13.5	0	0
Fourspot flounder	0	0	0	0	1.8	0.9	0	0	0	0
American plaice	0.8	0.1	1.1	<0.05	0	0	0	0	0	0
Wrymouth	0	0	0	0	1.8	0.9	0	0	0	0
Pollock	0.8	0.4	0	0	0	0	0	0	0	0
Filefish	0	0	0	0	0	0	0	0	2.1	0.5
Halfbeak	0	0	0	0	0	0	0.5	0.1	0	0
Longhorn sculpin	0	0	0	0	0	0	0	0	0	0
Unidentified fish	4.9	<0.05	3.2	<0.05	2.8	0.1	8.7	0.1	12.5	2.9
Spiny dogfish	0	0	10.8	3.7	2.8	16.6	0	0	0	0
Skate	0	0	0	0	9.2	9.3	0.5	0.3	0	0
Skate egg case	0	0	1.1	<0.05	1.8	<0.05	0	0	0	0
Squid	48.8	1.8	14.0	0.5	35.8	1.8	22.4	2.5	60.4	12.9
Octopus	0	0	0	0	0	0	0	0	2.1	0.5
Shrimp	0	0	0	0	0	0	2.7	<0.05	0	0
Lobster	0	0	0	0	1.8	0.5	0	0	0	0
Argonaut	0	0	0	0	0	0	0	0	4.2	0.4
Crab	0	0	0	0	0.9	<0.05	0.5	<0.05	0	0
Salp	0	0	0	0	1.8	0.1	0	0	0	0
Fig sponge	0	0	0	0	27.5	27.2	0	0	0	0
Finger sponge	0	0	0	0	0	0	0.5	<0.05	0	0

relation ($P<0.001$) between prey and bluefin tuna lengths was found for all prey-size data (Fig. 5). Despite this correlation, there appeared to be little association between predator and prey length for most species. The positive correlation was influenced by 29 larger prey items (>40 cm) all consumed by bluefin tuna larger than 230 cm. The larger prey were spiny dogfish, skate, bluefish, or Atlantic cod. Size data on the four most common prey species provided evidence of the consistency of prey size across a wide range of bluefin lengths in the Gulf of Maine. A significant positive size relationship was found for sand lance and Atlantic mackerel (both $P<0.001$), although both may have contained biases. The relationship for sand lance was influenced by smaller bluefin tuna that ate smaller sand lance (t-test, $P<0.001$) in Great South Channel than at Stellwagen Bank. All mackerel were YOY or age-1, except for two large mackerel consumed by larger bluefin tuna (>200 cm). The predator-prey size relationships for Atlantic herring ($P=0.36$) and squid ($P=0.16$) were not significant. A large majority (93%) of Atlantic herring prey were 18–27 cm in length, which corresponds to age-2 to age-4 cohorts for the western Gulf of Maine (Penttila et

Table 4

Summary statistics on stomach-contents biomass (g wet weight) from bluefin tuna caught at five seasonal feeding areas off New England, 1988–92. The geometric mean, confidence intervals (CI), and coefficient of variation (CV) are backtransformed from natural logarithms.

Statistic	All areas	Jeffreys Ledge	Stellwagen Bank	Cape Cod Bay	Great South Channel	South of Martha's Vineyard
Number of stomach samples with prey	568	123	93	109	183	48
Minimum stomach biomass	5	5	5	5	5	5
Maximum stomach biomass	16100	5800	6240	2900	16100	1200
Arithmetic mean	999	1957	1012	389	925	124
Geometric mean	214	832	438	133	126	37
Lower 95% CI	180	608	324	96	91	23
Upper 95% CI	255	1140	593	184	174	60
CV	39	26	24	35	46	44

al., 1989), and the youngest were age 2. There were no young-of-the-year (YOY) sand lance. Most sand lance from Great South Channel samples were age 2, in contrast to age 3 or age 4 at Stellwagen Bank (Weston et al., 1979). Most squid were YOY or age 1.

Numbers of prey species Few prey species were found in large numbers in a given stomach sample. Only sand lance, squid, Atlantic herring, and Atlantic mackerel had sample counts higher than 20 individual fish (Table 6). Data on prey numbers are limited because prey counts were made for only 208 samples. Many samples with large numbers of well-digested sand lance were difficult to count. From this subsample, the mean number of sand lance per stomach was 159, much higher than the next highest mean of 19 for Atlantic herring. Squid and mackerel commonly occurred as prey, although typically only a few individuals were found per stomach.

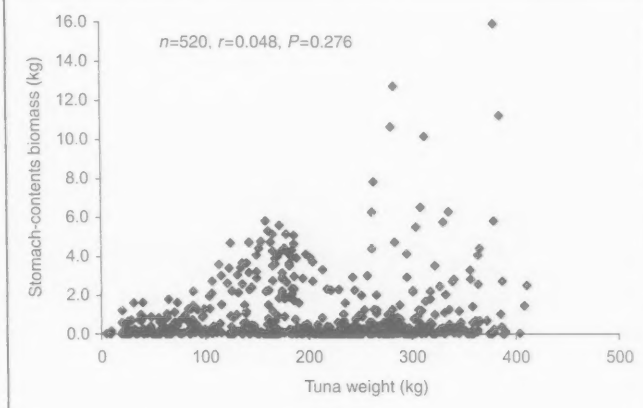

Figure 3

Scatterplot of bluefin tuna stomach-contents biomass and bluefin tuna weight for all samples from the Gulf of Maine, 1988–92.

Weight of prey species Sand lance and Atlantic herring (combined) accounted for 75% of the total stomach-contents biomass for all areas combined. The next highest species was bluefish at 7%. Despite a high frequency of occurrence, squid accounted a low percentage of overall biomass (2%) and a mean stomach prey weight of only 58 g. The highest mean prey weight was 1794 g for Atlantic herring. Only three other prey items averaged over 500 g in stomach-content weight: spiny dogfish (807 g), bluefish (742 g), and sand lance (661 g). With few exceptions, stomachs that were full or near full, contained only sand lance or Atlantic herring. Only five stomachs contained over 10 kg of prey contents: three with Atlantic herring, and one each with sand lance and Atlantic cod (16.0 kg, the largest meal observed).

In summary, five prey items occurred in frequency and mass to be considered important dietary components of the stomach contents sampled: sand lance, Atlantic herring, squid, Atlantic mackerel, and bluefish. Of these prey items, sand lance and Atlantic herring were the primary contributors to the diet of bluefin tuna sampled.

Discussion

Comparison of this study with previous west Atlantic bluefin tuna food habit studies revealed that fish prey represented a large majority of the diet, and cephalopods (primarily squid) were important secondary prey. Other prey taxa were minor components of the diet, except for Salpidae (Mason, 1976; Eggleston and Bochenek, 1990) and Amphipoda (Dragovich, 1970) for juvenile bluefin tuna. Comparisons with the four studies in which bluefin

tuna were sampled prior to 1970 (Crane, 1936; Krumholz, 1959; Dragovich, 1970; Matthews et al.[1]) were limited because of small sample sizes. In pre-1970 studies, sand lance or benthic organisms were not found to be prey items. Mason (1976) was the first to record sand lance in bluefin stomach contents. In three later studies, sand lance were found to be the most frequently occurring prey, followed by squid (Holliday, 1978; Eggleston and Bochenek, 1990; and the present study).

Two limitations common to previous diet studies were the small number of samples collected and the broad geographical range over which they were collected. In contrast, large numbers of samples were collected in the present study, at discrete feeding grounds on the New England continental shelf; moreover this study is the first in which the diet of bluefin tuna in the Gulf of Maine was quantified during their seasonal feeding migration. The major contribution of Atlantic herring and the common occurrence of demersal organisms as prey have not been previously recorded for bluefin tuna in the western North Atlantic Ocean.

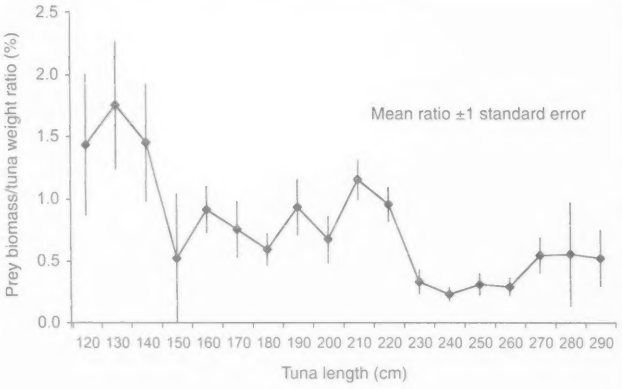

Figure 4

Relationship between the ratio of stomach-contents biomass to tuna weight (% wet weight [kg/kg]) and tuna length (curved fork length). All Gulf of Maine samples for bluefin lengths of 120–299 cm (n=519) were combined and arranged in 10-cm bins.

Sampling biases

Regurgitation, diel and seasonal effects, differential digestion rates, postcapture digestion, and predator size effects can be problematic to food habit studies and can bias data collection. (Bowen, 1986). This section discusses the potential effect that sampling biases may have on the findings of significant differences in the stomach-contents biomass and prey associations. A majority of the empty stomachs had distended stomach rugae, indicating that regurgitation had occurred. Similar observations were made during previous studies (Mason, 1976; and Dragovich, 1970), which would cause a negative bias for stomach-contents weight measurements. Diel and seasonal effects on feeding are difficult to assess and are large sources of variation. Large intersample variance can be expected given the complex interactions between predator populations and the temporal and spatial distribution of prey (Smagula and Adelman, 1982; Hodgson et al., 1989). Increasing sample size often may reduce variability, but high intra-

Table 5

Summary statistics for length data from major prey items in stomach contents and bluefin tuna sampled from Gulf of Maine (GOM), July–October, 1988–92. Prey lengths are total length, except for squid, which are mantle lengths. Bluefin tuna lengths are curved fork length (CFL). Area 1 = Jeffreys Ledge; area 2 = Stellwagen Bank; and area 4 = Great South Channel. n = number of samples taken.

		Prey				Bluefin tuna			
Species	Area	n	Mean (cm)	SD (cm)	Range (cm)	n	Mean (cm)	SD (cm)	Range (cm)
All prey	GOM	1866	17.7	7.27	3–80	190	220	38.60	104–297
Atlantic mackerel	GOM	150	15.9	3.27	10–36	40	215	42.56	132–272
Squid	GOM	89	13.8	5.63	3–24	41	224	30.81	159–295
Atlantic herring	GOM	364	24.6	2.51	18–31	57	211	30.19	119–276
Atlantic herring	1	263	24.4	2.65	18–31	42	209	27.83	119–276
Atlantic herring	4	91	25.1	1.94	21–30	9	221	42.05	130–272
Sand lance	GOM	1176	14.9	3.04	8–23	41	206	45.51	124–279
Sand lance	2	468	17.2	2.27	12–23	16	232	30.27	178–269
Sand lance	4	609	12.8	1.48	8–19	21	186	44.99	124–279

sample and intersample variation, prey weight skewness, and variance dependency are widespread findings in food habit studies that reflect natural feeding interactions (Smagula and Adelman, 1982; Amundsen and Klemetson, 1986; and Hodgson et al., 1989). Large sample variation was evident in the present study and limited the application of parametric statistics.

Differential digestion rates can result in an underestimate of the relative importance of a major prey item (Hyslop, 1980). Soft-bodied squid likely undergo digestion quicker than bony fish, and, therefore, prey weight measurements may have been negatively biased. Postcapture decomposition of prey has not been measured for bluefin tuna but may negatively bias stomach-contents weight for samples held a long time after capture (Holliday, 1978). The effect of bias on the prey weight data is suspected to be minor because of strong market incentives to chill harvested bluefin tuna and because samples were collected soon after capture.

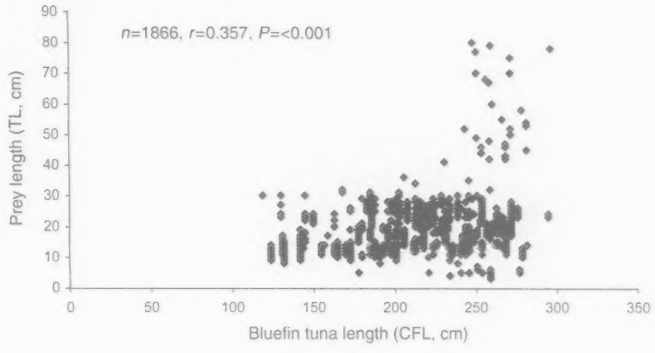

Figure 5

Relationship between bluefin tuna length and prey length for all Gulf of Maine samples during 1988–92 that contained measurable prey (190 stomach samples).

The separation of chum bait from natural prey and the exclusion of chum from diet analyses were potential minimal sources of bias. Because bluefin tuna swallow prey whole and chum is cut into small pieces, cut chum was readily separated from natural prey in stomach samples. Samples of small bluefin tuna that fed on the discards of trawlers in the area south of Martha's Vineyard did present a problem, and many of these samples were removed from analyses because natural prey and discards could not be distinguished. Other study areas did not indicate an association between tuna fisheries and trawl fishing; consequently, no evidence of discard feeding was observed. It is possible that the availability of chum could limit feeding on natural prey, although no evidence of this was found. Most chum was observed in the stomach contents of bluefin tuna from Stellwagen Bank and Jeffreys Ledge, but these areas also had the highest mean stomach-contents biomass and lowest frequency of empty stomachs.

Most of these biases were negative, possibly decreasing prey weight measurements in stomach contents, and could not easily be separated from natural conditions that lead to suboptimal feeding habits. Butler and Mason (1978) re-

Table 6

Prey number and prey weight data for the most common prey in stomach contents of bluefin tuna caught off New England during 1988–92. Both number of prey and prey weight were derived from all samples with prey (n=568), but prey number only includes samples where all prey could be counted.

	Number of prey			Prey weight (g)		
Prey species	n	Mean	Range	n	Mean	Range
Sand lance	25	159	2–557	194	661	5–10,590
Squid	76	3	1–28	186	58	5–1440
Atlantic herring	85	19	1–84	167	1794	5–12,700
Atlantic mackerel	27	6	1–30	108	175	5–1210
Bluefish	22	1	1–2	55	742	5–5800
Fig sponge	19	3	1–10	30	384	5–1250
Butterfish	10	2	1–5	21	80	5–450
Silver hake	1	17	—	16	93	5–250
Spiny dogfish	3	2	1–4	13	807	5–2900
Skate	9	1	1–2	13	359	50–810
Windowpane	11	1	1–3	12	158	40–250
Hake	5	2	1–3	11	227	40–640

ported higher daily consumption rates for pen-held bluefin tuna, an average of 28 kg per day during single feedings to satiation, and 40 kg per day during multiple feedings. Data from my study implied that naturally feeding bluefin tuna do not often reach these consumption rates: only five of 568 stomachs had prey contents over 10 kg. Regurgitation is a major confounding factor for stomach-contents biomass data and presents a serious challenge for calculations of daily rations and bioenergetic modeling of bluefin tuna feeding habits. The anatomy of the alimentary canal, combined with the stress of capture, appears to cause a high rate of regurgitation.

Cape Cod Bay

The bluefin tuna prey composition from Cape Cod Bay was unlike any prey composition previously reported for the west Atlantic, in that no individual prey item dominated nor was encountered at a high frequency of occurrence or percentage of stomach-contents biomass. In previous west Atlantic bluefin tuna food-habit studies, prey composition was dominated by a single, pelagic, schooling prey species (followed by a few secondary species of much less importance), and Pinkas (1971) reported similar results for Pacific bluefin tuna. Finding fig sponge as the highest ranked prey item in the diet of bluefin tuna in Cape Cod Bay was surprising; sessile prey organisms had not been found in previous bluefin tuna food-habit studies. Occurrence of fig sponge, locally known as "monkey dung," in the stomachs of bluefin tuna is commonly known to Cape Cod Bay fishermen who have questioned whether it is natural prey or whether it is accidentally swallowed during capture. I found the sponge at various stages of digestion; well-digested pieces as well as fresh pieces were found in the same stomach. The differential stages of digestion implies that fig sponge was ingested either as selected prey of unknown attraction and nutritional value or as incidental catch to a targeted bottom dweller.

Bottom foraging in the relatively shallow Cape Cod Bay (average depth: 25 m) was evident because eight of the 16 prey items identified were benthic or demersal species. Vertical excursions to the bottom in shallow regions were not unexpected, yet bottom foraging has not been reported for west Atlantic bluefin tuna. Bottom feeding was evident for most locations in this study, including foraging on small crabs (*Cancer* spp.) and finger sponge at Great South Channel where depths approached 100 m. In Cape Cod Bay, bottom foraging may not be the optimal feeding strategy for bluefin tuna and may simply be a response to low food availability, as suggested by the low prey biomass and higher proportion of naturally empty stomachs.

Prey size

To date, prey size in bluefin tuna food habit studies in the western North Atlantic has received little attention. Only Matthews et al.[1]) presented prey size data, a mean value based on 38 bluefin tuna stomachs. Young et al. (1997) found no relationship between prey size and size (40–192 cm) of juvenile southern Atlantic bluefin tuna (*Thunnus maccoyii*). I found only minor evidence of a predator-prey size relationship for bluefin tuna in the Gulf of Maine. A positive correlation was found between sand lance and bluefin length, although regional differences in the lengths of both species appears to bias the correlation. Smaller sand lance and bluefin tuna were found at Great South Channel than at Stellwagen Bank. A positive interaction between bluefin tuna and prey sizes was indicated by the consumption of the largest prey (>40 cm) by large bluefin tuna (>230 cm). Prey this large were not common in stomachs and were probably limited by mouth and esophagus gape. Otherwise, the sizes of prey were consistent across the range of bluefin tuna sampled in the Gulf of Maine.

The findings on prey size and numbers (per stomach) provide evidence of three selective foraging strategies used by bluefin tuna in the Gulf of Maine. Feeding on individual, fast-swimming pelagic prey was evident from consumed bluefish and Atlantic mackerel that are abundant pelagic species in the Gulf of Maine, but which occurred much less frequently in stomach contents and with few individuals per stomach. Ram feeding (swimming through a dense school prey with mouth open) of small prey may have resulted in high average number of sand lance found in stomachs and contributed to the similar prey sizes in most sizes of bluefin tuna. Bluefin tuna in Cape Cod Bay displayed a different foraging behavior, selecting larger, individual demersal prey. The variation in prey composition and different feeding strategies is consistent with previous descriptions of bluefin tuna as an opportunistic predator. However, the dominance of sand lance and Atlantic herring in the Gulf of Maine diet suggests a dependence on these species as an optimal energy source.

Trophic influences on bluefin tuna distribution

Changes in biomass and spatial availability of forage populations may affect the distribution of bluefin tuna on the New England continental shelf. Major changes in the prey community of the Gulf of Maine have occurred in recent decades. After Atlantic mackerel and Atlantic herring stocks off New England were severely overharvested in the 1960s and 1970s (NOAA, 1998), sand lance populations increased, presumably as a result of decreased predation and competition for food (Sherman et al., 1981). Atlantic herring and Atlantic mackerel stocks off New England increased steadily during the 1980s and 1990s (NEFSC, 1998). By the mid-1990s, the U.S. Atlantic coastal spawning stock biomass for these species increased to the highest levels on record (NEFSC, 1998).

Commercial bluefin tuna catches have increased in areas where Atlantic herring abundance has increased (western Gulf of Maine and Great South Channel) and diminished at traditional areas south of the Gulf of Maine (Chase, 1992). The northward shift in bluefin tuna distribution on the New England continental shelf may be influenced by improved foraging opportunities on Atlantic herring in the Gulf of Maine. I suspect that the timing of bluefin tuna migrations to the New England continental shelf are associated with seasonal spawning and feeding aggregations of Atlantic herring. Sand lance populations appear to be an important influence on bluefin tuna feeding migrations,

but they occur on a limited spatial scale in relation to Atlantic herring in the Gulf of Maine, and changes in their population abundance are not well documented. Atlantic herring and sand lance are also important in the diet and distribution of marine mammals in the Gulf of Maine (Payne et al., 1990; Weinrich et al., 1997; Gannon et al., 1998).

Changes in bluefin tuna stock composition and the long-term impact of small-mesh trawling gear on commercially important prey items (squid, silver hake, and butterfish) in southern New England waters and Mid-Atlantic areas where bluefin tuna catches have diminished are two potentially confounding factors in this discussion. In the management of Atlantic bluefin tuna, care should be taken to recognize that the fluctuations in the regional abundance of this species can be influenced by more than changes in stock structure. Changes in major prey populations, produced either by environmental features or by fishery practices, can have a profound effect on regional aggregations of bluefin tuna. Investigations should be conducted on introducing forage-base information into the interpretation of catch-per-unit-of-effort indices of abundance for Atlantic bluefin tuna populations. There is also a need for future research to improve our knowledge on the bioenergetics of this warm-bodied tuna and its associated relationships with prey species.

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Movement of American lobster (*Homarus americanus*) in the southwestern Gulf of St. Lawrence

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Abstract—A total of 42,445 American lobsters (*Homarus americanus*) were tagged in thirty-one sites throughout the southwestern Gulf of St. Lawrence between 1980 and 1997. Results from the recapture of 8503 tagged lobsters showed small distances traveled between the release and the recapture position for animals ranging in size from 51 to 152 mm carapace length. The average distance traveled ranged from 2 km in parts of Baie des Chaleurs and western Cape Breton to 19 km in central Northumberland Strait. Lobsters moved generally along the shore (93% of the dispersion was in areas between the shore and the 20-m bathymetric contour). As a result, lobsters traveled longer distances in sites characterized by a gradually sloping bottom where the distance between the shore and the 20-m contour line was extensive in contrast to areas characterized by rapidly changing depths and by a relatively small amount of habitat shallower than 20 m. In the majority of sites (14 of 19) there was no significant difference between males and females in the average distance they traveled. In four of the five sites females moved farther than males. In general, the average distance traveled by berried females was shorter than that traveled by males or nonberried females. No relationship was observed between the distance traveled and the size of the animal. There was no strong evidence of a relationship between the average distance traveled and the number of days at liberty. In general, lobsters in the southwestern Gulf of St. Lawrence traveled short distances and dispersion was restricted to the nearshore habitat. Further, the distance traveled was not correlated to size, sex, or years at large. These findings show that there is little interaction between American lobsters from different fishing areas at the benthic level and that American lobster movements should have minimal consequences for management of the species in the southwestern Gulf of St. Lawrence.

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The American lobster (*Homarus americanus* Milne-Edwards, 1837) fishery in the southwestern Gulf of St. Lawrence (GSL) and for the entire Canadian Maritime Provinces has become the most economically important fishery of coastal communities. Consequently, there is increasing interest by fishermen and the fishing industry to better understand the biology of the species and factors that may play a role in the fluctuations of landings, including possible lobster movements between lobster fishing areas (LFAs). Fishermen are particularly concerned by lobster movements because the minimal legal size increased in different LFAs in the southwestern GSL throughout the 1980s and 1990s, and they want to know whether lobsters returned at sea in a given area could be recaptured elsewhere.

Several tagging projects have been conducted in the past to study lobster movements in the GSL (Table 1). These tagging projects, initiated in the 1930s by Templeman (1935), showed that the average distance traveled by lobsters in the GSL was generally less than 15 km and that very few animals traveled up to 70 km (for review see Stasko, 1980; Lawton and Lavalli, 1995). Other tagging studies conducted in inshore waters outside the GSL in Nova Scotia (Wilder, 1974; Campbell, 1982, 1989; Campbell and Stasko, 1985; Miller et al., 1989; Tremblay et al., 1998), Bay of Fundy (Campbell, 1986; Campbell and Stasko, 1986), Maine (Cooper, 1970; Cooper et al., 1975; Krouse, 1981), New Hampshire (Watson et al., 1999), Massachusetts (Karnofsky et al., 1989) and Rhode Island (Fogarty et al., 1980) have also shown that lobster movements were generally similar (4 to 18 km) to those from the GSL. However, long-distance movements of more than 90 km for up to 20% of the animals have also been observed for lobsters tagged inshore (Dow, 1974; Fogarty et al., 1980; Campbell and Stasko, 1985, 1986; Campbell, 1989; Robichaud and Lawton, 1997); the farthest distance traveled reported was 798 km (Campbell and Stasko, 1986). These long distances traveled are more similar to those reported for offshore lobsters tagged on the continental shelf and over the offshore deep canyons (Saila and Flowers, 1968; Cooper and Uzmann, 1971; Uzmann et al., 1977; Fogarty et al., 1980; Campbell et al., 1984; Campbell and Stasko, 1985). Movements of more than 70 km have never been reported for lobsters tagged in the southwestern GSL.

Since 1980, forty-six tagging studies have been conducted throughout the southwestern GSL, mostly in areas where information on lobster movements has been unavailable. These tagging studies have covered fishing grounds characterized by a flat bottom and having a relatively smooth transition from shore to 30 m and a narrow habitat close to shore where changes in depths occur over a relatively short distance. The purpose of our study was to investigate the benthic movement of lobsters tagged in different locations within the southwestern GSL by comparing the distance traveled, number of days at liberty, and size and sex of lobsters.

Materials and methods

The recapture position was documented for 8503 lobsters, ranging in size from 51 to 152 mm carapace length (CL), from a total of 42,445 tagged and released during forty-six tagging studies in thirty-one sites throughout the southwestern GSL (Fig. 1) between 1980 and 1997 (Table 2). The animals were captured by traps and tagged between July and November after the commercial fishing seasons (May and June in LFAs 23, 24, 26A, and 26B, and from mid-August to mid-October in LFA 25). The CL, measured to the nearest mm, sex of each animal, and presence or absence of eggs under the female abdomen were recorded. Prior to 1989, all animals were tagged with orange sphyrion anchor tags, and blue streamer tags were used after 1992. Between 1989 and 1992 inclusively, both type of tags were used. A description of the tags and the tagging technique are presented in Moriyasu et al. (1995) and Comeau et al. (1998).

The positions of recaptured lobsters came from fishermen. Because all tagging projects were undertaken after each commercial fishing season, no lobsters were recaptured during the same year of their tagging. To increase fishermen's participation in reporting tagged animals, a major awareness campaign was conducted. Prior to 1993, representatives of the Department of Fisheries and Oceans (DFO) were present at each wharf to measure and collect information on tagged lobsters that were recaptured. Beginning in 1993, letters were sent to all lobster fishermen in regions where tagging projects were conducted; in these letters the tagging project was described, in-

Table 1

Locations and authors of lobster tagging studies on movements of American lobster (*Homarus americanus*) conducted in the Gulf of St. Lawrence.

Location	Authors and date
Various locations in Gulf of St. Lawrence	Wilder (1974)
West coast of Newfoundland	Templeman (1940)
Magdalen Islands (Québec)	Templeman (1935)
	Bergeron (1967)
	Munro and Therriault (1983)
Gaspé Peninsula (Québec)	Corrivault (1948)
Malpeque (Prince Edward Island)	Templeman (1935)
Western Prince Edward Island	Wilder (1963)
Northumberland Strait	Templeman (1935)
	Wilder (1963)

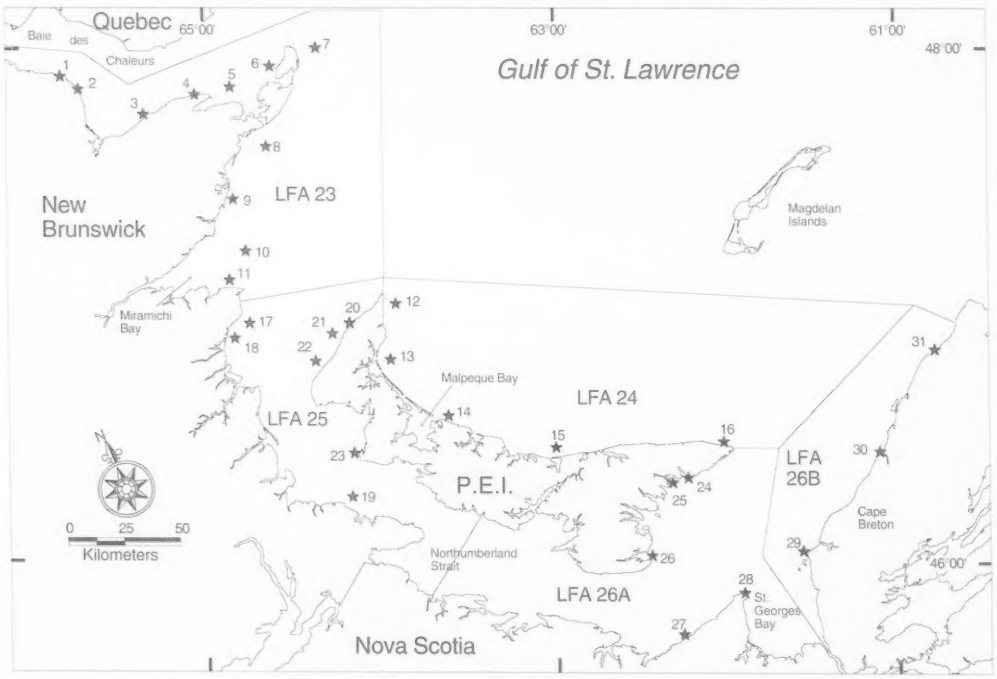

Figure 1

Locations (★) of American lobster (*Homarus americanus*) tagging studies conducted in the southwestern Gulf of St. Lawrence between 1980 and 1997. The names of each site are presented in Table 2. The lobster fishing areas (LFAs) are indicated on the map.

structions given for returning lobster tag information, and the cooperation of the fishermen was sought (Comeau et al., 1998). Similar information was posted at wharves. For each tagged lobster, fishermen were asked to record date of capture, tag number, position of capture, and depth. They were then asked to freeze the animal with the tag still attached and contact an information collection center, where they could leave their names, addresses, and telephone numbers. A DFO representative collected tagged lobsters for measurement and reimbursed fishermen according to the market value of the recovered lobsters. No reward was issued. Fishermen also had the option to bring the lobsters and the information to a fisherman-representative. If a tagged lobster under the legal size or a tagged berried female was captured, fishermen were asked to record the above information and release the lobster to the water with the tag still attached.

The distance traveled by each recaptured animal was calculated as the linear distance between release and recapture positions. The Kruskal-Wallis and Mann-Whitney (*U*-test) tests were used to compare the average distance traveled for males, females, and berried females for ani-

Table 2

Average distances traveled by American lobsters tagged in the southwestern Gulf of St. Lawrence between 1980 and 1997. The number of each site corresponds to its geographical position on the map in Figure 1. *n* = number of recaptured lobster with tags indicating release location for which distance traveled to recapture site could be calculated.

Tagging site	Year of tagging	*n*	Average carapace length ±SD (mm)	Carapace length range (mm)	Average distance traveled ±SD (km)
1 Belledune	1980	604	70.5 ±4.9	50–115	7.4 ±6.5
2 Pointe-Verte	1996	26	78.2 ±6.4	71–90	6.1 ±4.0
3 Stonehaven	1994–97	618	73.2 ±5.4	53–111	2.4 ±3.0
4 Anse-Bleue	1994	290	73.5 ±4.8	54–91	3.5 ±6.3
5 Caraquet	1993–97	1416	74.2 ±9.2	55–133	8.0 ±8.8
6 Petit-Shippagan	1994	134	76.2 ±10.4	54–116	8.7 ±8.8
7 Miscou	1995	58	69.9 ±8.2	66–117	4.5 ±6.5
8 Le Goulet	1996	101	73.8 ±6.2	59–98	5.3 ±3.5
9 Val Comeau	1985, 1996–97	519	76.3 ±9.1	57–117	7.0 ±6.5
10 Néguac	1996	74	78.0 ±8.7	65–105	14.2 ±8.2
11 Escuminac	1997	17	73.9 ±5.2	66–88	9.6 ±9.9
12 Seacow Pond	1996	62	71.1 ±6.0	61–94	5.3 ±7.8
13 Alberton	1996	62	74.0 ±6.9	65–97	5.7 ±5.9
14 Malpeque	1989	492	68.1 ±7.2	51–100	10.1 ±7.0
15 Tracadie	1984	27	68.1 ±12.4	55–111	10.4 ±10.1
16 North Lake	1996	78	72.8 ±5.0	61–89	2.5 ±3.4
17 Pointe-Sapin	1996	22	72.5 ±5.0	65–83	6.7 ±4.1
18 Kouchibouguac	1997	53	67.7 ±4.3	60–74	8.0 ±7.3
19 Cap-Pelé	1997	41	72.2 ±6.0	60–84	12.2 ±11.9
20 Skinner's Pond	1996	13	71.4 ±5.8	63–131	5.4 ±6.7
21 Miminegash	1996	37	74.1 ±8.5	64–100	8.6 ±10.8
22 Howard's Cove	1995	79	66.9 ±7.1	54–84	15.3 ±13.2
23 Egmont Bay	1982	15	66.1 ±7.0	58–77	19.4 ±16.0
24 Souris	1996	213	75.4 ±7.1	59–109	4.9 ±6.8
25 Fortune	1996	208	72.7 ±3.9	66–84	3.3 ±3.6
26 Beach Point	1982	243	88.0 ±12.9	61–120	7.4 ±8.9
27 Lismore	1997	51	78.2 ±11.4	58–103	7.8 ±12.4
28 Ballantynes Cove	1986	226	74.0 ±11.2	55–130	9.3 ±13.0
29 Port Hood	1988	339	67.4 ±11.6	51–150	4.5 ±2.9
30 Margaree	1984, 1988, 1992	1332	70.7 ±8.5	52–152	3.2 ±5.1
31 Pleasant Bay	1988, 1992	1053	69.8 ±8.1	54–130	2.3 ±2.1

mals recovered during the first recapture period following their tagging. Correlation (r) was used to determine the relationship between the distance traveled and the size of the animal. To determine the relation between the average distance traveled and days at liberty, sites with recaptures over multiple years were used. The relationship between the average distance traveled and the extent of shallow waters was also established. The extent of shallow waters was quantified as the distance from shore to the closest 30-m bathymetric contour for each tagging site.

Results

A total of 7565 tagged lobsters were returned during their first recovery period, with size and geographical position at recapture. Only sites with fifty recaptures or more were considered. There was no evidence of a relationship between the size of the animal and distance traveled in the southwestern GSL because the correlation coefficient (r) ranged from –0.19 to 0.23 (Table 3). In this study, small lobsters (<70 mm CL) traveled as far as the large animals (>90 mm CL) (Fig. 2).

Table 3

Correlation coefficient (r) for the relationship of the distance traveled and the carapace length (CL) of American lobsters tagged in the southwestern Gulf of St. Lawrence. The number of each site corresponds to its geographical position on the map in Figure 1. n = number of recaptured lobster with tags indicating release location for which distance traveled to recapture site could be calculated.

Tagging site	n	CL range (mm)	r
1 Belledune	536	50–115	–0.12
3 Stonehaven	580	53–111	0.04
4 Anse-Bleue	232	54–91	0.02
5 Caraquet	1288	55–133	0.08
6 Petit-Shippagan	117	54–116	0.10
8 Le Goulet	90	59–98	–0.03
9 Val Comeau	500	57–117	–0.05
10 Neguac	72	65–105	0.22
12 Seacow Pond	61	61–94	0.08
13 Alberton	61	65–97	–0.08
14 Malpeque	251	51–100	0.11
16 North Lake	64	61–89	0.18
18 Kouchibouguac	51	60–74	–0.06
22 Howard's Cove	73	54–84	–0.19
24 Souris	202	59–109	0.14
25 Fortune	207	66–84	0.04
26 Beach Point	243	61–120	–0.02
27 Lismore	51	58–103	0.13
28 Ballantynes Cove	188	55–130	0.23
29 Port Hood	339	51–150	0.20
30 Margaree	1319	52–152	–0.05
31 Pleasant Bay	1040	54–130	0.04

There was no significant difference in the average distance traveled between males and females in eleven out of nineteen sites (Table 4). Females traveled significantly farther than males (Table 4) at three sites located in the upper part of Baie des Chaleurs (Fig. 1, sites 1, 3, and 4) and one site on the northeastern tip of Prince Edward Island (Fig. 1, site 25). The only site where males traveled significantly farther than females was in Val Comeau (Table 4, Fig. 1, site 9). No significant differences were observed in the average distance traveled by berried females compared with males or nonberried females in four out of nine sites where data were available for berried females (Table 4). The average distance traveled by berried females was significantly shorter than that by both males and females in three sites (Table 4, sites 9, 16, and 25) and significantly farther only in Port Hood (Table 4, site 29). In Souris (Table 4, site 24), no significant difference was observed for average distance traveled between males and berried females, but they were both significantly shorter than the average distance traveled for nonberried females.

Only seven out of thirty-one sites had a sufficient number of recaptures over multiple years to allow a comparison between distance traveled and days at liberty. A substantial decrease in the percentage of tags recaptured from the first to the second and third recovery periods was observed (Table 5), reflecting high exploitation rates by the fishery. There is no strong evidence of a positive relationship between the average distance traveled and days at liberty. No significant difference (P>0.05) was observed in the average distance traveled over time in Stonehaven (site 3), Anse-Bleue (site 4), Caraquet (site 5) and North Lake (site 16) (Table 5). The average distance traveled decreased significantly (P=0.0002) in Belledune (site 1), whereas it increased significantly in Souris (site 24) (P=0.0119) and Margaree (site 30) (P=0.004) over multiple years recovery (Table 5). Even in these areas where distances were significantly different, the differences were not large (2.4, 2.3, and 5.3 km). Also, the longest distance traveled observed for the second or third (or both) recovery periods was equal or less than the one observed for the first recovery period for all 7 sites (Table 5).

Lobster movements in the southwestern GSL seemed to be restricted to short distances along the coast near shore in areas where the lobster habitat is restricted to a few kilometers from the shore and longer distances over a broader gradually sloping bottom (Fig. 3). In general, 93% of lobster dispersions were limited to the 20-m bathymetry contour. The shorter average distances traveled (2.4–4.9 km, Table 2) were observed in part of Baie des Chaleurs (Figs 1 and 4, sites 3 and 4), the northeastern tip of Prince Edward Island (Fig. 1, sites 16, 24, and 25) and Cape Breton (Figs 1 and 5, sites 29, 30, and 31). Relatively short average distances (5.3–8.6 km, Table 2) were observed around northeastern New Brunswick (Figs 1 and 6, sites 1, 2, 5, 6, 8, and 9), the northwestern tip of Prince Edward Island (Fig. 1, sites 12, 13, 20, and 21), eastern New Brunswick (Fig. 1, sites 17 and 18) and the eastern end of

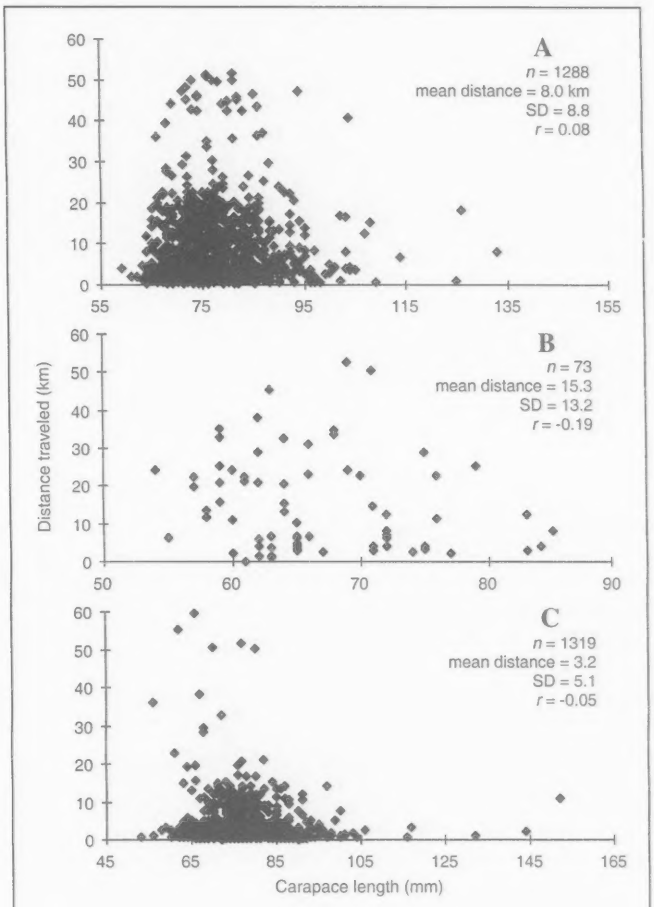

Figure 2

Relationship between the distance traveled and the size of the animal for American lobsters recaptured in (**A**) Caraquet, (**B**) Howard's Cove, and (**C**) Margaree.

the Northumberland Strait (Fig. 1, sites 26 and 27). The longest average distances traveled (9.3–19.4 km, Table 2) were observed in the immediate vicinity of Miramichi Bay (Figs 1 and 6, sites 10 and 11), Malpeque Bay and Tracadie Bay in northern Prince Edward Island (Fig 1, sites 14, and 15), St. Georges Bay (Fig. 1, site 28) and central Northumberland Strait (Figs 1 and 7, sites 19, 22, and 23).

Lobster movements in the Northumberland Strait were related to whether the site was located toward the center or at either extremity (either end) of the Strait. Lobsters at sites close to the external boundaries (Fig. 1, sites 17, 18, 20, 21, 26, and 27) traveled on average shorter distances (5.4–8.6 km) than those located in the center of the Strait (Fig. 1, 12.2–19.4 km, sites 19, 22, and 23). Although tags were recovered in the western portion of Northumberland Strait (LFA 25) at a different time (a different fishing season) compared with tag recoveries at the other LFAs, movements seemed to be related to the extent of shallow waters (<20 m) rather than the time of the recovery period.

Discussion

Lobster movements in the southwestern GSL are related to the local bottom topography and are depth-dependent, i.e. lobsters traveled on average longer distances in areas where the shallow waters (<20 m) extended farther from shore. We observed that on the narrow coastal shelf of western Cape Breton and in some areas in Baie des Chaleurs, lobsters traveled on average less than 5 km compared with distances ranging from 9.3 to 19.4 km in the gradually sloping bottom of the Northumberland Strait and some shallow bays. Similarly, Templeman (1935) reported

Table 4

Comparison of the average distance traveled between the average distance traveled by male, female, and berried female American lobsters. The number of each site corresponds to its geographical position on the map in Figure 1. *n* = number of recaptured lobster with tags indicating release location for which distance traveled to recapture site could be calculated.

Tagging site	Biological category	*n*	Average distance traveled ±SD (km)	*U*-Test or Kruskal-Wallis[1] *P*
1 Belledune	male	360	7.0 ±5.9	0.0003
	female	176	9.0 ±8.3	
3 Stonehaven	male	316	2.1 ±2.8	0.0248
	female	264	2.7 ±3.3	
4 Anse-Bleue	male	127	2.1 ±3.3	0.0056
	female	105	3.8 ±5.2	
5 Caraquet	male	746	8.1 ±9.1	0.0937
	female	487	7.7 ±8.6	
	berried female	55	5.5 ±6.6	
8 Le Goulet	male	45	5.3 ±2.7	0.4385
	female	45	5.2 ±2.7	
9 Val Comeau	male	279	7.7 ±7.1	0.0260[2]
	female	218	6.3 ±5.6	
	berried female	5	1.3 ±0.7	0.0018
12 Seacow Pond	male	20	5.0 ±7.7	0.5800
	female	41	5.5 ±7.9	
13 Alberton	male	33	6.0 ±6.7	0.8849
	female	29	5.4 ±5.0	
14 Malpeque	male	114	11.0 ±7.6	0.7310
	female	95	11.2 ±7.4	
	berried female	42	10.5 ±9.9	
16 North Lake	male	26	2.1 ±1.4	0.4700[2]
	female	33	3.5 ±4.9	
	berried female	5	0.8 ±0.6	0.0243
18 Kouchibouguac	male	25	8.9 ±7.8	0.5847
	female	26	8.0 ±7.0	
22 Howard's Cove	male	43	17.3 ±12.3	0.1333
	female	31	12.8 ±14.0	
24 Souris	male	131	3.6 ±5.3	0.5826[3]
	female	66	7.1 ±9.0	0.0140[2]
	berried female	5	1.6 ±0.7	0.0355
25 Fortune	male	133	3.2 ±3.6	0.0155[2]
	female	62	4.0 ±3.7	
	berried female	12	0.5 ±0.2	0.0001
26 Beach Point	male	178	6.4 ±6.2	0.4729
	female	65	10.1 ±13.4	
28 Ballantynes Cove	male	56	8.5 ±10.0	0.6193
	female	132	8.0 ±9.7	
29 Port Hood	male	139	4.4 ±3.1	0.7616[2]
	female	158	4.3 ±2.6	
	berried female	42	5.6 ±3.2	0.0294
30 Margaree	male	449	3.1 ±4.9	0.1478
	female	553	3.5 ±5.0	
	berried female	317	2.8 ±5.0	
31 Pleasant Bay	male	322	2.1 ±1.8	0.2638
	female	565	2.3 ±2.2	
	berried female	153	2.5 ±2.4	

[1] The *U*-test and the Kruskal-Wallis test were used to compare two and three groups, respectively.
[2] *U*-test between males and females.
[3] *U*-test between males and berried females.

Table 5

The average and the longest distances traveled by American lobsters for sites with tags returned over multiple years. The time between tagging and recapture of the animal (number of days at liberty), and the number of observations (n) are indicated. The number of each site corresponds to its geographical position on the map in Figure 1.

Tagging site	Number of days at liberty	n	Average distance traveled (km)	U-test or Kruskal-Wallis[1] P	Longest distance traveled (km)
1 Belledune	295–378	497	7.6 ±6.1	0.0002	44
	678–747	72	6.7 ±7.5		37
	1048–1102	35	5.2 ±3.9		17
3 Stonehaven	231–291	580	2.4 ±3.0	0.5827	28
	598–648	38	2.4 ±4.1		17
4 Anse-Bleue	217–270	235	2.9 ±4.3	0.2753	32
	577–628	48	6.2 ±11.9		56
	942–972	7	5.0 ±7.3		17
5 Caraquet	213–360	1302	7.9 ±8.4	0.6416	51
	584–725	97	7.7 ±11.8		49
	965–1057	17	11.8 ±14.5		50
16 North Lake	232–280	65	2.7 ±3.7	0.2075	24
	605–641	13	1.7 ±1.5		6
24 Souris	230–285	202	4.7 ±6.9	0.0119	31
	584–625	11	7.0 ±4.2		13
30 Margaree	250–308	147	3.3 ±3.7	0.004	23
	622–671	13	8.6 ±7.6		21

[1] The U-test and the Kruskal-Wallis test were used to compare two and three groups, respectively.

that the average distance traveled by lobsters from sites located on the north side of Prince Edward Island and the western part of the Northumberland Strait ranged from 7 to 10 km. As with our results, longer movements were reported in the Egmont Bay area (central Northumberland Strait); lobsters traveled an average distance of approximately 14 km (Wilder, 1963) on lobster habitat in shallow (<20 m) waters. In other sites within the GSL, lobsters also traveled on average small distances. Lobsters in the Magdelan Islands (Templeman, 1935; Bergeron, 1967) and on the northern shore of Baie des Chaleurs (Corrivault, 1948) traveled average distances ranging from 3 to 16 km and 12 km or less, respectively. On the west coast of Newfoundland, Templeman (1940) reported that lobsters traveled an average of 3.2 km in St. George's Bay and 8.2 km in Port-au-Port Bay; hence, lobsters disperse within the GSL, in general, over small distances in inshore waters.

Most of the lobster movements observed in the southwestern GSL were oriented along the coast in inshore waters. Although the shallow (<20 m) gradually sloping bottom of the central Northumberland Strait, the Malpeque Bay, and Miramichi Bay areas allows for longer and more broader dispersions, lobsters remain close to either the New Brunswick, Nova Scotia, or Prince.Edward Island coastline, or confined to a bay environment. However, dispersions along the coast might not be the only types of lobster movements in southwestern GSL. Movements perpendicular to the coast have been documented in the Magdalen Islands (Templeman, 1936; Bergeron, 1967; Munro and Therriault, 1983), Bonavista Bay in Newfoundland (Ennis, 1984), and on the north shore of Baie des Chaleurs (Corrivault, 1948) because a migration of lobsters moving inshore in the spring and offshore in the fall was observed.

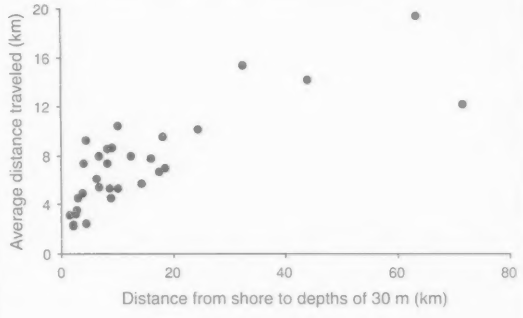

Figure 3

Relationship between the average distance traveled and the extent of shallow waters measured by the distance from shore to the closest 30-m bathymetric contour.

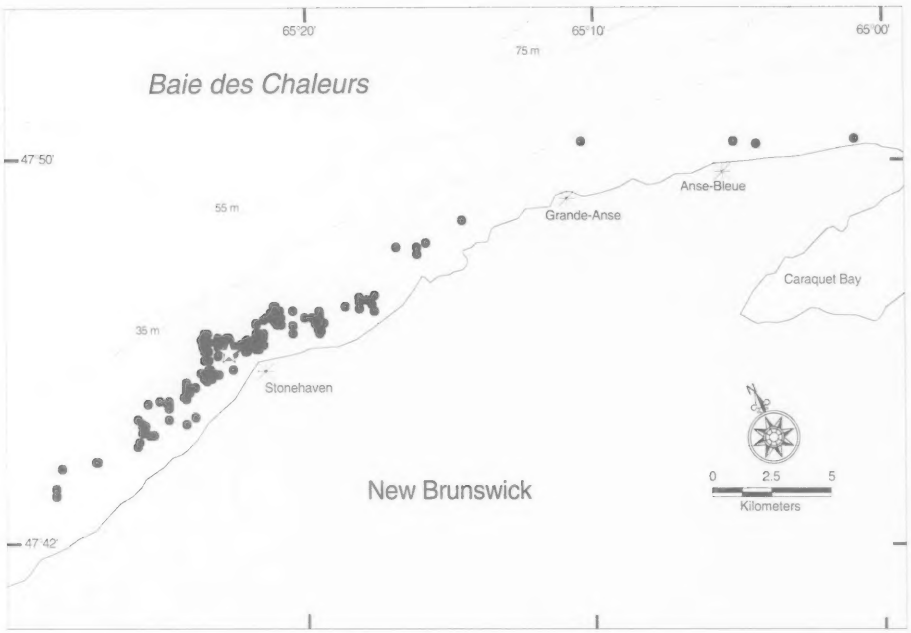

Figure 4

Locations (•) of tagged American lobsters recaptured in 1995 and 1996 (n=296) from the 1994 tagging project conducted in Stonehaven, New Brunswick. The release sites are indicated by a star symbol.

Recently, a trawl survey conducted at a depth of 40 m in the Caraquet area (Baie des Chaleurs) over a 7-month period produced lobsters in mid-May, late-October, and November, but not between June and early-October (Comeau, personal obs.). Further, the recapture positions during the fishing season showed that lobsters tagged during these trawl surveys were recaptured along the coast at depths less than 20 m from Stonehaven to Miscou (Comeau, personal obs.). This finding suggests that there is an inshore–offshore movement on the south shore of Baie des Chaleurs similar to the one observed by Corrivault (1948) on the north shore of that bay. Unfortunately, our tagging projects were not designed to study this type of movement and did not allow us to speculate more on inshore–offshore movements.

The lack of long-range movements across the southwestern GSL could be explained by the presence of an extensive cold (<1.5°C) intermediate layer (CIL). In the southwestern GSL, the CIL is a large volume of water sandwiched between the coastal water and the deep water located in the Laurentian channel. The top of the layer ranges from 20 to 40 m depth from June to October and rises to the surface from January to April (Gilbert and Pettigrew, 1997). As it was hypothesized by Stasko (1980), there seems to be no advantage in long-distance movement to deeper water (>40 m) for lobsters in the GSL because it is cold (<1.5°C) in both summer and winter (CIL). Although lobsters can tolerate temperatures ranging from –1.5° to 30°C, at temperatures below 0°C they are in a state of hibernation, and below 5°C molt induction is blocked (Waddy et al., 1995). It is clear that lobsters can "tolerate" cold temperature but to be active they need warmer waters. Lobster movements of more than 40 km were rare in the southwestern GSL and movements exceeding 70 km through deep, colder waters (>40 m) were not observed. In contrast, lobsters from the Bay of Fundy, from coastal waters of southwestern Nova Scotia, and from coastal waters off New England can take advantage of warmer temperatures in deep waters in the Gulf of Maine and on the continental shelf during the winter (Campbell and Stasko, 1986). Campbell and Stasko (1985) and Campbell (1989) showed that lobsters tagged in the inshore waters of southwestern Nova Scotia traveled up to 240 km to the edge of the continental shelf off Georges Bank to depths below 200 m, seemingly without crossing a wide area of cold water. Similarly, lobsters tagged in the Bay of Fundy were also recaptured in deep waters at the edge of the continental shelf across the Gulf of Maine and along the coastal waters of the United States (Campbell and Stasko, 1986), at a distance of more than 780 km. These types of movements were not observed in the southwestern GSL. Lobster movements between mainland New Brunswick, Prince Edward Island, or Cape Breton, and the Magdalen Islands, for example, have not been reported. The Magdalen Islands are an archipelago with a substantial lobster fishery located in the middle of the southwestern GSL, surrounded by >60 m depths at about 80 to 90 km from Prince Edward Island, and Cape Breton. Lob-

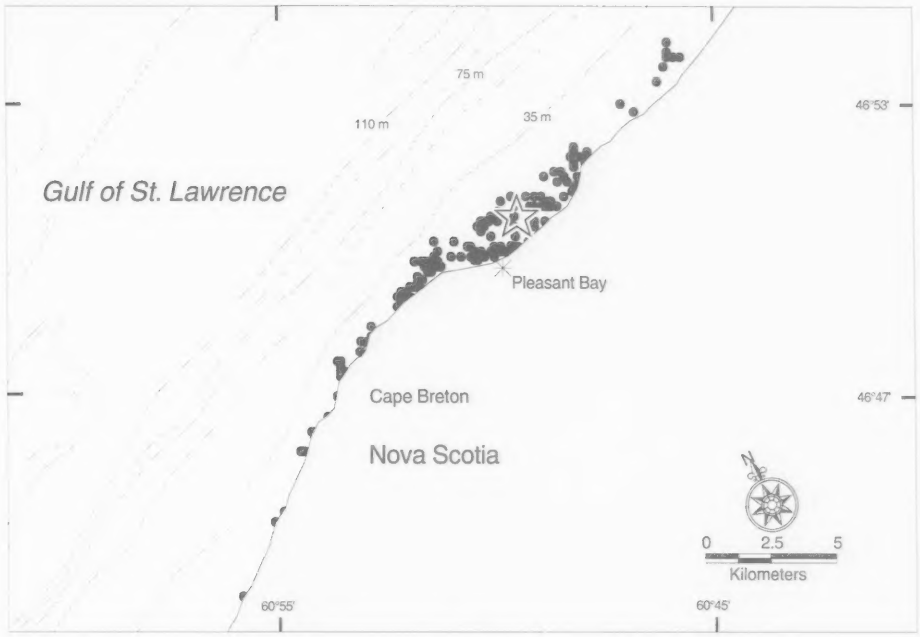

Figure 5

Locations (•) of tagged American lobsters recaptured in 1993 (n=777) from the 1992 tagging project conducted in Pleasant Bay, Nova Scotia. The release sites are indicated by a star symbol.

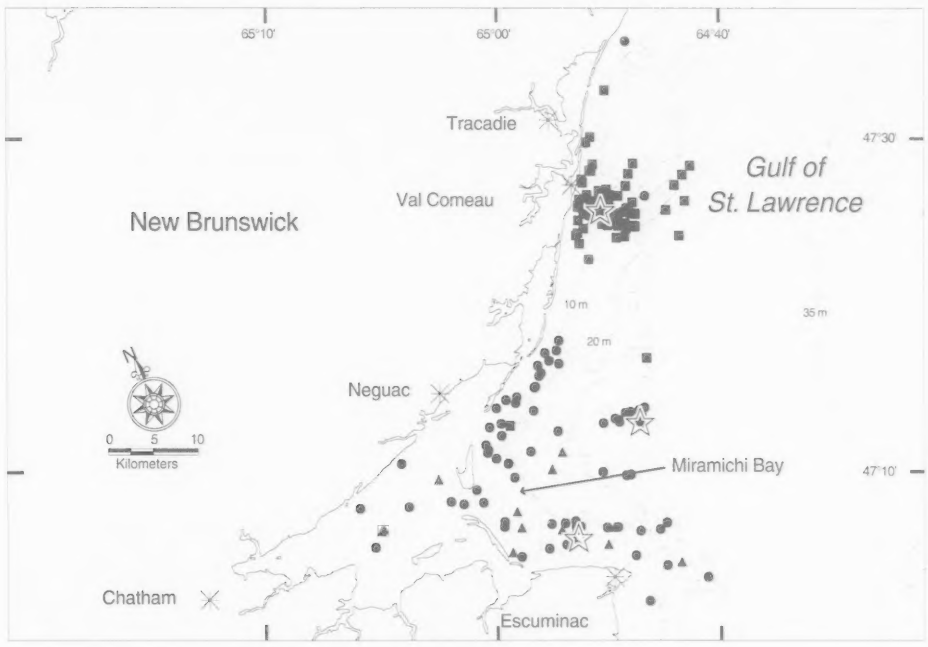

Figure 6

Location of tagged American lobsters recaptured in the Val Comeau and the Miramichi Bay area. Squares represent lobsters recaptured from the 1996 Val Comeau (n=127) tagging project, circles represent lobsters recaptured from the 1996 Neguac (n=74) tagging project, and triangles represent lobsters recaptured from the 1997 Escuminac (n=17) tagging project. The release sites are indicated by a star symbol.

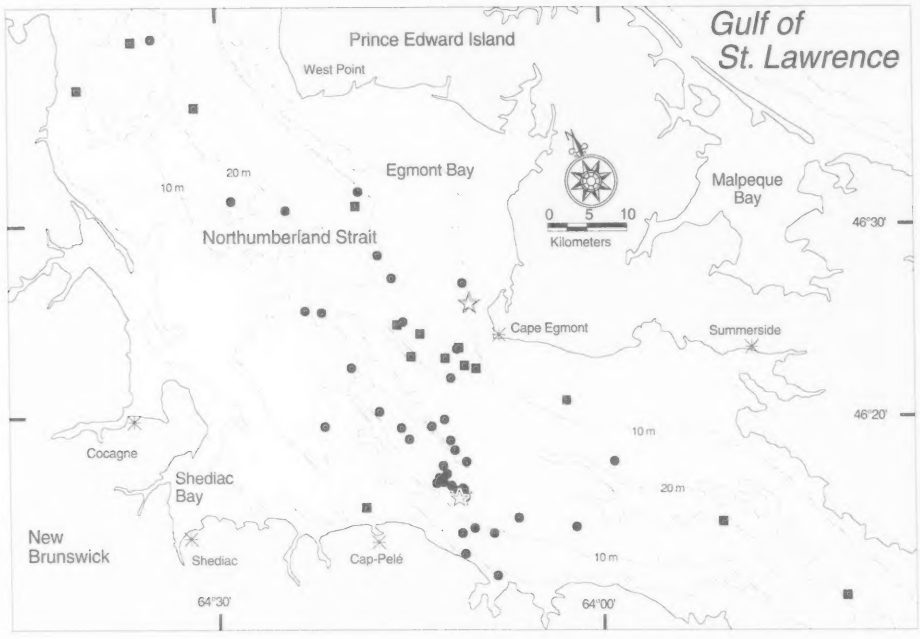

Figure 7

Location of tagged American lobsters recaptured in central Northumberland Strait. Squares represent lobsters recaptured from the Egmont Bay (n=15) tagging project and circles represent lobsters recaptured from the Cap-Pelé (n=41) tagging project, conducted in 1982 and 1997, respectively. The release sites are indicated by a star symbol.

ster movements in the southwestern GSL seem to be temperature-dependent because the cold waters of the CIL appeared to be an effective barrier to movements between the shallow waters of the Magdelan Islands and the shallow coastal waters of the rest of the southwestern GSL.

The distances traveled by lobsters (>60 mm CL) in the southwestern GSL were not sex- or size-dependent, except for berried females. Similar to our findings, the results of most recent studies do not indicate significant differences between the distance traveled in relation to size or sex for lobsters tagged in coastal waters (Fogarty et al., 1980; Krouse, 1981; Campbell, 1982; Tremblay et al., 1998). In contrast, Templeman (1935) and Bergeron (1967) suggested that lobster movements were sex-dependent, but neither author reported whether the differences were supported in a statistical or biological sense. Campbell and Stasko (1985, 1986) and Campbell (1989) indicated that lobster movements were size-dependent because they observed that large mature animals (≥95 mm CL) on average traveled significantly farther than small immature ones. They explained that mature animals would move more extensively to reach the warmest seasonal temperature to maximize their degree-days (the accumulative sum of daily mean temperatures recorded above 0°C) needed for somatic and gonadic development. This was not the case in our study. We observed, however, that on average berried females in the southwestern GSL traveled shorter distances than males and nonberried females. Saila and Flowers (1968) indicated that the distance traveled by berried females was related to their physiological state. In a tagging experiment, they captured berried females on the continental shelf, tagged, and released them in the inshore waters off the coast of Rhode Island at about 220 km from their captured position. When females were carrying eggs, they traveled only short distances within the inshore waters. Once they shed their eggs, however, these females returned to the continental shelf where they were originally captured. Berried females tagged in inshore waters in the Magdalen Islands (Munro and Therriault, 1983), Jeddore Harbour and Clam Bay, Nova Scotia (Jarvis, 1989), and New Hampshire (Watson et al., 1999) also traveled short distances. In the Cape Cod area, berried females tagged in the inshore waters were reported to have traveled an average distance of 30 km, mostly parallel to the coast (Morrissey, 1971; Estrella and Morrissey, 1997). Off Grand Manan Island, Campbell (1986, 1990) reported relatively small inshore–offshore migration, less than 15 km, for 75% of the berried females and attributed this migration to an effort to maximize egg development by exposure to warmer water. In general, it seems that the condition of carrying eggs could influence the extent of movements in the southwestern GSL, not the size or sex of the animal.

In terms of fishery management, there is relatively little interaction between lobsters at different LFAs at the benthic level because lobster traveled on average small

distances. The main concern of fishermen in the southwestern GSL was the minimal legal size (MLS) disparity between LFA 24 (MLS of 63.5 mm CL) located on the north side of Prince Edward Island and the other LFAs (MLSs from 65.1 to 70.0 mm CL). More precisely, they were interested in lobster movements in relation to time, i.e. if lobsters released in a given area in one season would be recaptured in the same area in future seasons. From our findings, lobsters do not move farther if they are at large for a longer period. Distances traveled by lobsters were not time-dependent for lobsters at large between 200 (with at least one winter season) and 1102 days. Results of our tagging studies were consistent with results from earlier studies carried out in the southwestern GSL and demonstrated that lobsters in their benthic stages have little long distance interaction. Hence, lobster movements in the southwestern GSL should have minimal consequences in terms of lobster management.

Acknowledgments

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Shortspine thornyhead (*Sebastolobus alascanus*) abundance and habitat associations in the Gulf of Alaska

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Abstract–Shortspine thornyhead (*Sebastolobus alascanus*) abundance was estimated from 107 video transects at 27 stations recorded from a research submersible in 1991 off southeast Alaska at depths ranging from 165 to 355 m. Numbers of invertebrates in seven major taxa were estimated, as was substrate type. Thornyhead abundance ranged from 0 to 7.5/100 m^2, with a mean of 1.22/100 m^2, and was positively correlated with depth and amount of hard substrate. Invertebrate abundances were not significantly correlated with numbers of thornyheads. Shortspine thornyhead abundance estimates from this study were several times higher than estimates produced by bottom trawl surveys off southeast Alaska in 1990 and 1993, the two years of survey that encompassed the submersible transects; however, the trend of increasing abundance with depth was similar in the trawl surveys and in the submersible transects, suggesting that trawl surveys systematically underestimate abundance of shortspine thornyheads.

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Fish distributions are affected by physical conditions such as depth, temperature and substrate type and by biotic variables such as prey distribution, predator presence, and habitat features (e.g. kelp forests). Patterns of habitat use are important factors in resource assessments, and stratification based on habitat characteristics are common features of survey design. For example, trawl surveys in the Gulf of Alaska are stratified by depth and general bottom type (flats, gullies, shelf break, slope) (Stark and Clausen, 1995). Assessment of fish populations based on traditional fishing gear, such as trawls or longlines, provide relatively economical surveys with broad geographic coverage; however, they provide limited detailed information on species associations or habitat preferences (Matlock et al., 1991).

Shortspine thornyhead (*Sebastolobus alascanus*) is a member of the family Scorpaenidae, which includes the rockfishes (*Sebastes*—over 60 species in the northeast Pacific) and three species of thornyheads (*Sebastolobus*). Shortspine thornyhead range from Baja California, Mexico, to the Bering Sea and are found at depths to 1500 m (Moser, 1974). Off southeast Alaska, most fish sampled from 200–310 m depths were between 15 and 30 years old and had lengths of 25–35 cm (Miller, 1985). The maximum age observed by Miller (1985) was 62 years, and age at 50% maturity was 12 years for both sexes. These life-history features are similar to those of rockfishes, and such long-lived fishes are difficult to manage because they are easily overexploited and recover slowly from overfishing (Adams, 1980). Shortspine thornyhead have been commercially valuable in the Gulf of Alaska, where catch (including discards) ranged from 1298 to 2020 metric tons from 1991 to1996 (Ianelli and Ito[1]). Bycatch of thornyhead has the potential of forcing closure of other high-value fisheries (Ianelli and Ito[2]). Estimates of their abundance and size distribution are currently based on bottom trawl and longline surveys (Ianelli and Ito[2]); however, direct observations from submersibles can provide an alternate method for assessing abundance (Krieger, 1993). Assessments of thornyheads and rockfishes often result in population estimates with high variances; resulting in considerable uncertainty for assigning

[1] Ianelli, J. N., and D. H. Ito. 1998. Status of Gulf of Alaska thornyheads (*Sebastolobus* sp.) in 1998. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, p. 371–402. [Available from North Pacific Fishery Management Council, 605 West 4th St., Anchorage, Alaska 99501.]

[2] Ianelli, J. N., and D. H. Ito. 1994. Thornyheads. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska for 1995. [Available from North Pacific Fishery Management Council, 605 4th St., Anchorage, Alaska 99501.]

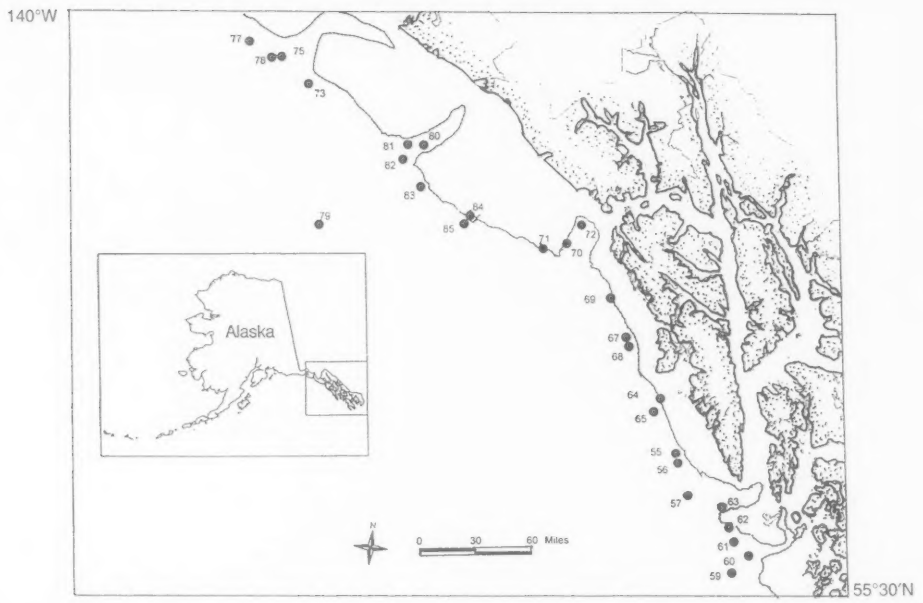

Figure 1

Locations of stations (•) where transects were run off southeast Alaska. The offshore line marks the 200-m isobath near the edge of the continental shelf.

harvest levels. Submersible observations with line-transect methods have been used in attempts to improve estimates of rockfish abundance and to understand rockfish habitat associations (Richards, 1986; Pearcy et al., 1989; Krieger, 1992; Stein et al., 1992; O'Connell and Carlile, 1993).

Our goal was to assess abundance and habitat use by shortspine thornyhead in the eastern Gulf of Alaska, based on data from existing video records taken during submersible transects. We estimated abundance of fish and invertebrates and quantified substrate type. We explored the relationships between thornyhead abundance and both physical and biotic environmental variables and compared abundance estimates from submersible transects with those from trawl surveys in the same area.

Materials and methods

Sources of data were video tapes of 107 bottom transects recorded at 27 stations during submarine dives in June 1991 on the outside coast of northern southeast Alaska from Cape Ommaney to Yakatat (Fig.1). All transects were conducted with the Delta submersible. This battery-powered two-man submersible is 4.7 m long, dives to 365 m, and travels 2–6 km/h. It is equipped with ten 150 W external halogen lights, internal and external video cameras, a 35-mm external camera, magnetic compass, directional gyro compass, and underwater telephone and transponder that allowed the submersible to be tracked from the surface support vessel. The surface vessel recorded LORAN fixes at the beginning and end of each transect. A pilot and observer formed the crew of the submersible: the pilot attempted to maintain the submersible within 0.5 m above the bottom at 3–4 km/h while the observer made observations through a starboard porthole.

Video recordings were made from a downward projecting external Hi-8 color video camera tilted obliquely forward on the starboard side and included a digital readout of depth, temperature, and height above bottom. Data were collected either in strip transects by using the entire length of each transect, or in quadrats by freezing individual frames from the video. The width of the strip transect was calculated from the height above bottom and field of view of the camera. The field of view formed a trapezoid on the seafloor beginning almost directly beneath the camera and projecting forward; its maximum width (W) was estimated by calibrations performed on a subsequent cruise that had the same camera and camera configuration (Zhou and Shirley, 1997). When the submarine was resting on the bottom, the camera height (H) was 0.93 m and the width of the field of view (i.e. longest side of trapezoidal field) was 1.78 m. Transect width (W) was estimated by

$$W = (1.78/0.93)\,H, \qquad \text{[(Zhou and Shirley, 1997)]}.$$

The height above bottom (H) was recorded at one minute intervals during each transect and mean height was used to estimate width (W) of that transect. All dives were made during daylight between 0600 and 1900 h. At each station a series (usually 4) of parallel transects was run, and spacing between transects was about 200 m. Transect lengths

were calculated from the position fixes taken from the surface vessel.

The entire length of each transect was viewed and all thornyheads in the field of view were counted. Invertebrates were also counted in seven categories: starfish, seapens, sea urchins, anemones, corals, sponges, and sea cucumbers. Depth and temperature were recorded once every minute during each transect and averaged over the complete transect. Substrate type was estimated by scoring video quadrats at one-minute intervals during the transect. A mylar grid of about twenty-five 50-mm squares was placed on the screen over the freeze-framed image, and substrate within the squares was scored in three categories of soft (mud, sand, and gravel), cobble, and rock-boulder, the latter two of which were then combined into a single category, hard-bottom. The proportions of each category (soft and hard) for each transect were estimated as the mean from the one-minute quadrats. Abundance (number/100 m^2) of shortspine thornyheads and invertebrate categories was estimated for each transect by dividing the number counted by the area estimate ($W \times$ *Transect length* $\times$ 100).

To evaluate variables that may have affected thornyhead densities, we assembled a correlation matrix and a partial correlation matrix of three physical variables (depth, substrate, temperature) and transformed ($\log(x+1)$) biotic variables (shortspine thornyheads and seven invertebrate categories). Based on those matrices, we selected depth and substrate for further analyses.

We used nonparametric procedures (Kruskal-Wallis and Mann-Whitney) to determine if thornyhead densities varied among sampling stations and to evaluate the effects of substrate and depth. Substrate and depth were coded into nominal categories for use as independent variables in those analyses. We used Scheffe's (Zar, 1984) *post-hoc* test to evaluate between-category differences when Kruskal-Wallis results were significant.

An ANOVA factorial model was used to explore the joint effects depth and substrate on shortspine thornyhead abundance (transformed by $\log(x+1)$). In addition, we used stepwise linear regression with thornyhead abundance as the dependent variable to evaluate the relative importance of all possible independent variables.

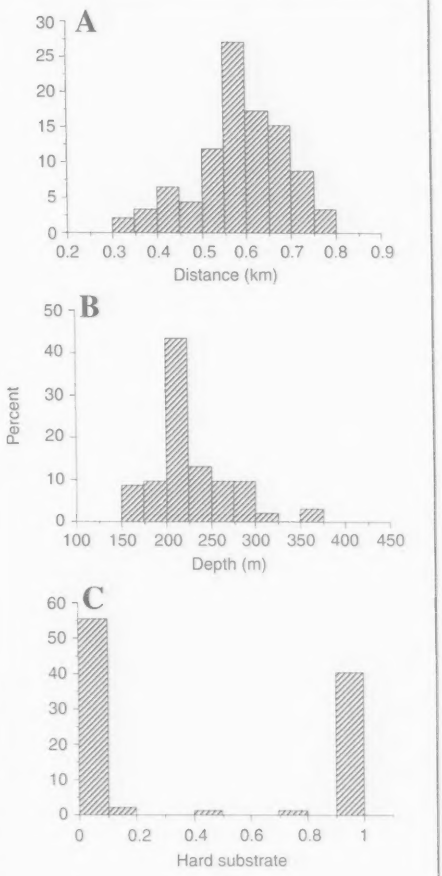

Figure 2

Distribution of transects by (**A**) distance (km), (**B**) average depth, and (**C**) the proportion of bottom categorized as hard.

Results

Transect lengths ranged from 320 to 800 m and had a mean of 580 m (Fig. 2A). The mean transect depth ranged from 165 to 355 meters, and the highest numbers of transects were at 200–250 m (Fig. 2B). Most transects (85%) had substrate that was completely soft (silt, sand, and gravel) or hard (cobble and rock-boulder) (Fig. 2C). Abundance of shortspine thornyheads per transect ranged from 0 to 13.6/100 m^2; and the mean abundance at the 27 stations ranged from 0 to 7.5/100 m^2 (Table 1). Difference in abundance among stations was very highly significant (P <0.0001, Kruskal-Wallis).

A correlation matrix of all variables indicated that depth, substrate, and sponge abundance were related to variation in thornyhead abundance; however, the partial correlation matrix indicated that among those three variables, substrate type and depth were most strongly related to shortspine thornyhead abundance (Table 2). The high correlation of sponge and thornyhead abundances was apparently spurious because of the relationship between sponge abundance and substrate type (Table 2).

For further analyses of the relationship between thornyhead abundance, depth, and substrate, we coded depth into three nominal categories, <200 m, 200–300 m, and >300m, chosen to correspond to the depth intervals used in National Marine Fisheries Service (NMFS) triennial trawl surveys (Stark and Clausen, 1995). We also coded substrate into two nominal categories, soft bottom (>90% sand, mud, and gravel) and hard bottom (>40% cobble and rock-boulder). Abundance increased with depth (Table 3), and differences that were highly significant occurred among three depth categories (P<0.001, Kruskal-Wallis). Significant differences exist-

Table 1

Mean numbers, with standard deviation, of shortspine thornyheads (*Sebastolobus alascanus*) per 100 m^2 at transect stations, with means of depth, bottom temperature, and proportion of the bottom categorized as hard substrate.

Station	*n*	No./100 m^2	SD	Mean depth (m)	Temp.	Proportion of bottom as hard substrate	Lat.	Long.
55	4	0.4	0.002	210.1	4.00	0.27	56°37′11″	135°57′50″
56	4	0.5	0.002	209.0	4.33	0.00	56°32′19″	135°54′39″
57	4	2.7	0.007	319.9	3.83	1.00	56°06′06″	135°39′72″
59	4	0.2	0.002	280.1	4.51	0.00	55°46′03″	134°77′97″
60	4	0.0	0	227.9	4.83	0.00	55°61′28″	134°55′86″
61	4	0.0	0	202.9	4.90	0.00	55°71′53″	134°76′89″
62	4	0.0	0	165.5	5.42	1.00	55°86′00″	134°84′00″
63	4	0.9	0.004	355.9	4.04	0.04	55°98′36″	134°93′97″
64	4	3.8	0.011	220.3	4.86	0.78	56°80′97″	135°80′97″
65	4	2.5	0.007	237.9	4.73	0.54	56°69′22″	135°87′69″
67	3	2.6	0.012	247.9	3.95	0.11	57°24′72″	136°29′31″
68	4	3.6	0.02	246.2	4.50	0.75	57°21′67″	136°25′03″
69	4	7.5	0.045	242.7	4.53	0.72	57°55′33″	136°55′22″
70	4	0.7	0.01	217.7	4.84	0.20	57°95′94″	137°21′61″
71	4	0.1	0.002	177.4	4.95	1.00	58°02′00″	137°10′00″
72	4	0.1	0.001	289.9	4.02	0.00	58°10′92″	136°98′39″
73	4	1.2	0.007	210.8	4.79	1.00	59°03′75″	141°13′75″
75	4	0.1	0.001	208.4	4.25	0.86	59°24′50″	141°62′14″
77	4	2.9	0.015	299.8	3.76	0.71	59°31′44″	142°11′42″
78	4	0.0	0	205.8	4.25	0.77	59°22′22″	141°70′86″
79	4	0.0	0	183.9	4.67	0.51	58°00′00″	140°50′00″
80	4	0.4	0.001	251.4	4.43	0.00	58°66′81″	139°37′33″
81	4	0.3	0.002	208.4	5.04	0.00	58°65′61″	139°56′08″
82	4	0.3	0.001	262.8	4.59	0.00	58°53′81″	139°61′56″
83	4	0.0	0	218.9	4.81	0.00	58°35′00″	139°32′89″
84	4	0.0	0	172.4	5.32	0.76	58°22′00″	139°00′00″
85	4	2.4	0.016	215.2	5.26	0.74	58°10′17″	138°65′33″

ed between the shallowest depth category and both deeper depth groups (Table 3, Sheffe test). Substrate type also affected abundance (Table 3); transects with hard substrate had a significantly higher density of thornyheads than transects on soft bottom (P=0.016, Mann-Whitney). There was a significant interaction (P=0.01) of depth and substrate in the ANOVA factorial analysis (Table 4) due to the sharp increase in thornyhead abundance in depths >200 m on the hard substrate than on the soft substrate (Fig. 3).

Stepwise multiple regression with all variables resulted in a model that incorporated two variables: substrate type and depth, with substrate type entered first. The final two-variable regression model was

$$A = 0.017\,S + 0.00016\,D - 0.033, \qquad [r^2=0.208]$$

where A = thornyhead abundance;
S = proportion of bottom that is hard substrate; and
D = depth (m).

Thornyhead abundance increased with depth and amount of hard substrate, although there was an indication that abundance may have reached maximum levels at depths of 200–300 m (Fig. 3).

Discussion

Film (still or motion) and videotape recordings of transects have been used to assess abundance of aquatic organisms (Auster et al., 1989; Butler et al.[3]). Potential biases in such data include systematic underestimation

[3] Butler, J. L., W. W. Wakefield, P. B. Adams, B. H. Robison, and C. H. Baxter. 1991. Application of line transect methods to surveying demersal communities with ROVs and manned submersibles. Proceedings of the IEEE Oceans '91 Conference, p. 689–696. Institute of Electrical and Electronic Engineers, Piscataway, NJ.

Table 2

Correlation (lower left diagonal) and partial correlation matrices (upper right diagonal) for shortspine thornyhead (SSTH), depth, substrate type, temperature, and invertebrates. Significant correlations are indicated in bold.

	SSTH	Depth	Substrate	Temperature	Sea star	Urchin	Sea pen	Anemone	Coral	Sponge	Cucumber
SSTH		0.35	0.37	0.08	−0.13	0.24	0.04	−0.13	0.04	0.27	−0.12
Depth	**0.23**		−0.34	−0.56	0.02	0.03	0.00	0.09	−0.16	−0.08	0.11
Substrate	**0.32**	**−0.31**		0.00	−0.12	−0.16	−0.01	0.39	−0.15	0.23	0.25
Temp.	−0.10	**−0.62**	0.17		−0.02	−0.07	0.24	0.04	−0.05	−0.15	−0.22
Seastar	−0.18	0.05	−0.16	−0.04		0.23	0.18	0.24	0.04	−0.06	0.01
Urchin	0.11	0.18	**−0.21**	−0.12	**0.35**		0.19	0.04	0.08	−0.13	−0.04
Sea pen	−0.01	−0.09	0.04	0.13	**0.36**	**0.33**		−0.06	0.35	0.10	0.43
Anemone	0.00	−0.07	**0.38**	0.03	**0.22**	0.04	0.15		0.07	0.07	0.09
Coral	−0.05	−0.09	−0.03	0.03	**0.30**	**0.27**	**0.61**	0.16		0.05	0.27
Sponge	**0.37**	−0.08	**0.41**	−0.02	−0.18	−0.16	−0.02	0.14	−0.04		−0.17
Cucumber	−0.06	0.08	0.13	−0.15	0.27	0.20	**0.59**	**0.24**	**0.53**	−0.09	

Table 3

Mean abundance (number/100 m^2) of shortspine thornyheads in three depth categories (Kruskal-Wallis, $P<0.0001$), and in two substrate categories (Mann-Whitney, $P=0.016$), with sample sizes and standard errors. Results of nonparametric analyses are included.

	Abundance	*n*	SE
Depth			
100–200	0.1	18	0.1
200–300	1.4	80	0.2
>300	1.9	9	0.4
Substrate			
soft	0.6	57	0.1
hard	1.9	50	0.4

Table 4

Factorial analysis of effect of depth and substrate (proportion of bottom categorized as hard substrate) on shortspine thornyhead abundance (number/100 m^2, $\log(x+1)$ transformed).

Variable	df	Sum of squares	*F*-value	*P*
Depth	2	1.01	10.28	<0.0001
Substrate	1	0.35	7.10	0.009
Depth-substrate interaction	2	0.41	4.17	0.018
Residual	101	4.96		

due to gear avoidance or overestimation due to attraction of fish to the submersible. The behavior of shortspine thornyheads observed in the videotapes from our study indicated that they were not affected by the submersible. They typically remained relatively motionless unless the submersible came very close (almost touching the fish). It is also unlikely that they had moved away, or toward, the submersible, before coming into the camera field. On all dives there was an observer and another video camera recording a broader area, and there was no indication that shortspine thornyheads were responding to the submarine. The passive behavior of shortspine thornyheads in response to submersibles has been noted previously (Krieger, 1992).

In transect assessments, the probability of detecting organisms typically is not equal over the entire field of view. Detection is affected by such factors as lighting, orientation of the organism and its reflectivity, sea floor relief, suspended particles, and size of the organism. Butler et al.[3] examined the detection functions for three types of fish (flatfish, hagfish, and thornyhead) from data collected off California. For thornyheads, the probability of detection was relatively constant to a distance of about 180 cm. This distance is larger than the width of the transects in our study, indicating that our use of a constant detection function (probability of 1.0) was appropriate.

We found that shortspine thornyheads preferred habitat with hard substrate. Submersible transects have been used to identify habitat used by rockfishes and thornyheads in the northeast Pacific Ocean (Richards, 1986; Pearcy et al., 1989; Stein et al., 1992; O'Connell and Carlile, 1993; Krieger and Ito, 1999). Off Oregon, thornyheads were included in an assemblage of fishes associated with mud bottom (Stein et al., 1992), and Pearcy et al. (1989) observed that in deep water they occurred on mud bottom, but in shallower water were found over both rock and mud. We have no explanation for the differences in habitat association between Oregon and southeast Alaska.

Our observations are based on a larger number of transects than those surveyed off Oregon, but the consistency of results from the two Oregon studies suggests that the difference is not due to a low sample size there. Our observation that abundance of shortspine thornyheads increases with depth is consistent with results from trawl surveys off Alaska, Oregon, and California (Martin and Clausen, 1995, Stark and Clausen, 1995, Jacobson and Vetter, 1996). Off Oregon, their abundance was highest in the 200–400 m depth zone, and decreased sharply between 400 m and 1400 m (Jacobson and Vetter, 1996). Off California, the highest abundance of shortspine thornyheads occurred at 400–600 m, probably because of the warmer waters off California (Jacobson and Vetter, 1996). Thus, our sampling depths covered the most important depth zones for this species in the waters off southeast Alaska, which are colder than those off Oregon.

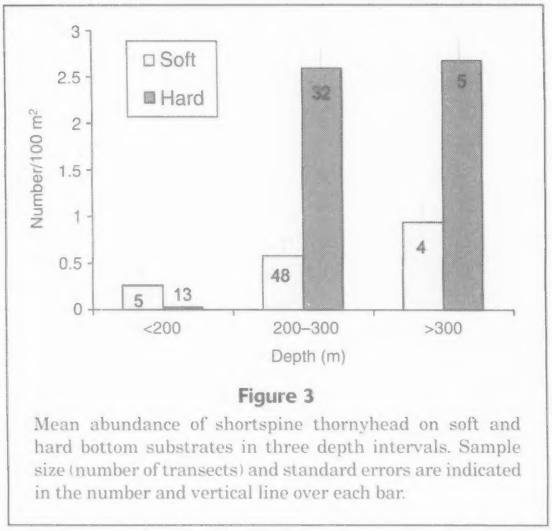

Figure 3

Mean abundance of shortspine thornyhead on soft and hard bottom substrates in three depth intervals. Sample size (number of transects) and standard errors are indicated in the number and vertical line over each bar.

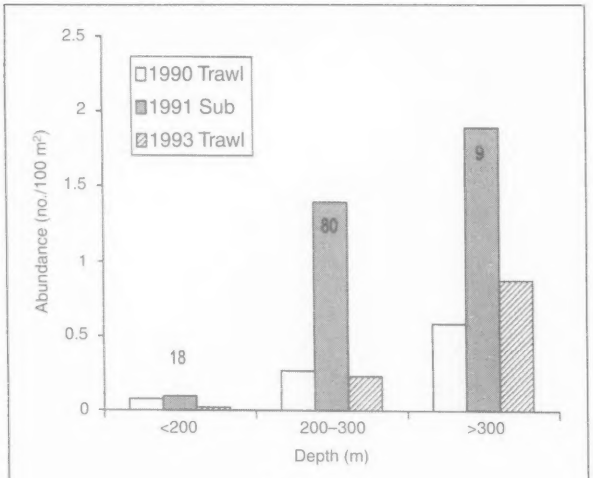

Figure 4

Mean abundance of shortspine thornyhead in three depth intervals from submersible transects in 1991 and from the 1990 and 1993 trawl surveys off southeast Alaska. Sample size (number of transects) and standard errors of the submersible estimates are indicated in the number and vertical line with each bar.

Bottom trawl surveys of fishes in the Gulf of Alaska are conducted triennially, and occurred one year before (1990) and two years after (1993) our submersible survey (Martin and Clausen, 1995; Stark and Clausen, 1995). For many species, trawl survey results may be biased because some species may be herded by the trawl doors into the path of the net, resulting in overestimates of abundance when the "area-swept" method is applied (Krieger, 1992). Other fish in the water column above the bottom may swim over the net and be underestimated by the survey (Balsiger et al., 1985). Escape routes under the foot rope and through the larger meshes in the trawl wings are also possibilities.

The NMFS trawl survey does not cover exceptionally rugged rocky habitats that would destroy equipment; consequently, species that select high-relief habitats may be underestimated by the survey, whereas species that select low-relief soft-bottom habitats may be overestimated. Submersible observations provide a means to quantify the biases inherent in bottom trawl surveys. The depth categories we used to analyze the submersible data matched the depth strata used in the NMFS triennial trawl surveys. Mean abundance of shortspine thornyheads in submersible surveys were several times higher that those in the 1990 and 1993 trawl surveys; however, the ratios of abundance in the three depth zones were very similar (Fig. 4). We suggest that trawl surveys underestimate the abundance of shortspine thornyheads in the Gulf of Alaska but may be good indicators of relative abundance, patterns of distribution, and stock trends.

Acknowledgments

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Geographic and temporal patterns in size and maturity of the longfin inshore squid (*Loligo pealeii*) off the northeastern United States

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Abstract–Analysis of 32 years of standardized survey catches (1967–98) indicated differential distribution patterns for the longfin inshore squid (*Loligo pealeii*) over the northwest Atlantic U.S. continental shelf, by geographic region, depth, season, and time of day. Catches were greatest in the Mid-Atlantic Bight, where there were significantly greater catches in deep water during winter and spring, and in shallow water during autumn. Body size generally increased with depth in all seasons. Large catches of juveniles in shallow waters off southern New England during autumn resulted from inshore spawning observed during late spring and summer; large proportions of juveniles in the Mid-Atlantic Bight during spring suggest that substantial winter spawning also occurs. Few mature squid were caught in survey samples in any season; the majority of these mature squid were captured south of Cape Hatteras during spring. Spawning occurs inshore from late spring to summer and the data suggest that winter spawning occurs primarily south of Cape Hatteras.

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Fish. Bull. 200–213 (2002).

The longfin inshore squid, *Loligo pealeii*, is distributed in the northwest Atlantic from Canada to the Caribbean (Cohen, 1976). Within its range of commercial exploitation (from southern Georges Bank to Cape Hatteras) the population is considered to be a unit stock (NEFC[1]), although heterogeneous subpopulations may exist (Garthwaite et al., 1989).

North of Cape Hatteras, *L. pealeii* migrate seasonally. The migration has been described as a movement offshore during late autumn (so that the species can overwinter in warmer waters along the edge of the continental shelf) and a return movement inshore during the spring and early summer (Summers, 1969; Serchuk and Rathjen, 1974; Tibbetts, 1977). Murawski (1993) defined *L. pealeii* as a member of a migratory, warm-water group of species, centered primarily in mid-Atlantic waters (particularly in the spring), that make inshore and northward migrations in the spring and offshore and southward migrations in late autumn.

Geographic patterns in Northeast Fisheries Science Center (NEFSC) survey catches, from the Gulf of Maine to Cape Hatteras, show that *L. pealeii* are distributed over the entire continental shelf (from inshore to offshore) in the autumn, are concentrated at the edge of the continental shelf and at the southern end of the survey area during winter and spring, and are concentrated inshore in summer (Summers, 1967; 1969; Serchuk and Rathjen, 1974; Vovk, 1978; Lange, 1980; Whitaker, 1980; Lange and Waring, 1992).

Analyses of survey catches indicate that depth, time of day, and temperature all influence cross-shelf distribution patterns (Summers, 1969; Serchuk and Rathjen, 1974; Lange and Waring, 1992; Murawski, 1993; Brodziak and Hendrickson, 1999). Diel correction factors have been applied to survey indices in various studies to adjust nighttime bottom trawl catches to daytime equivalents (daytime catches are higher when squid are concentrated close to the bottom) (Lange and Sissenwine1983; Lange and Sissenwine[2]). Research by Lange and Waring (1992) and Brodziak and Hendrickson (1999) demonstrated that the diel differences were size specific and that further consideration of these differences in correction factors was warranted.

Until recently, *L. pealeii* was thought to have a life span of up to three years, and the stock was assessed accordingly (Sissenwine and Tibbetts, 1977; Lange, 1981; Lange and Sissenwine,

[1] NEFC (Northeast Fisheries Center). 1986. Report of the second NEFC stock assessment workshop. NEFC Lab. Ref. Doc. 88-02, 114 p. [Available from NEFSC, 166 Water Street, Woods Hole, MA 02543.]

[2] Lange, A. M. T., and M. P. Sissenwine. 1977. *Loligo pealei* stock status. Northeast Fisheries Science Center Lab. Ref. Doc. 77-28, 9 p. [Available from NEFSC, 166 Water Street, Woods Hole, MA 002543.]

1983; Lange[3]; Lange et al.[4]). Recent advances in the use of statoliths for age determination of squid (see reviews in Rodhouse and Hatfield, 1990; Jereb et al., 1991; Jackson, 1994) have enabled new estimates of life span to be derived for *L. pealeii* (Macy, 1995; Brodziak and Macy, 1996; Macy[5]), which indicate that the life span of *L. pealeii* can be less than nine months. Back-calculations of hatching date from age data revealed that there is more than just a spring-summer spawning component of the population (Brodziak and Macy, 1996; Macy[5]), with a small proportion of squid hatching during winter. This winter spawning is presumed to occur offshore (Brodziak and Macy, 1996), in the vicinity of the submarine canyons along the edge of the northeastern U.S. continental shelf, from Hudson Canyon up to Georges Bank (Fig. 1). The possibility of winter spawning was raised initially by Summers (1969), based on length-frequency data, but squid were not presumed to spawn until their second year because their growth was assumed to be too slow to allow spawning during their first summer.

Our study reports on two studies: 1) an analysis of survey data from spring and autumn NEFSC surveys from 1967 to 1998, and from winter NEFSC surveys from 1992 to 1998, to describe gross distribution patterns of *L. pealeii* over the northwest Atlantic continental shelf from Cape Hatteras to the Gulf of Maine; 2) some results of a field study initiated in 1997 to investigate geographic and seasonal patterns of growth and maturity to determine if the winter spawning component off the northeastern United States can be defined by time and area.

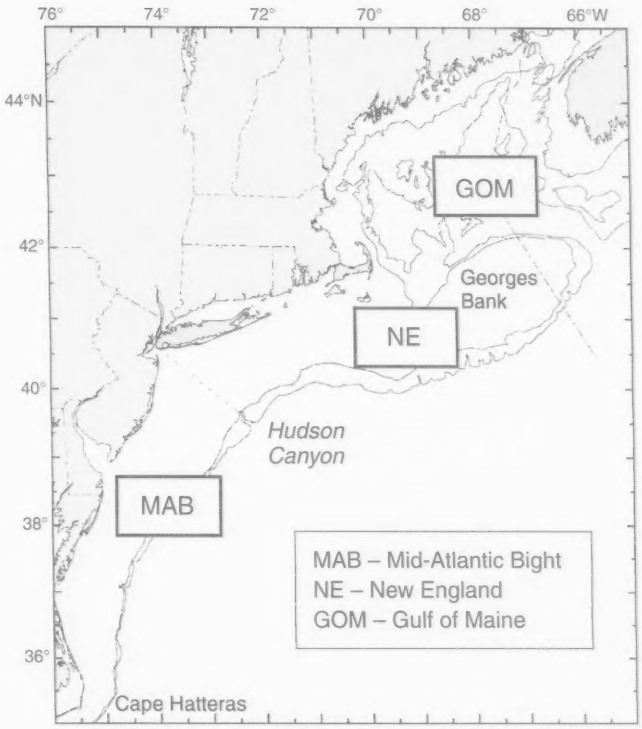

Figure 1

Map of the survey areas for longfin inshore squid off the northeastern coast of the United States (1967–98).

Materials and methods

Survey analysis

Length-frequency data for *L. pealeii* were analyzed from NEFSC bottom-trawl surveys conducted in the autumn (generally from mid-September to late October) from 1967 to 1997; in the spring (generally from March to early April) from 1968 to 1998; and in the winter (generally in February) from 1992 to 1998. Data collection and processing and archiving methods are described by Azarovitz (1981). In the autumn and spring surveys the same trawl-sampling gear (Yankee-36 trawl) has been used since 1967, except during 1973–81, when a Yankee-41 (high rising) trawl was substituted in the spring surveys. In the winter surveys the trawl gear was larger and the Gulf of Maine was not sampled.

The NEFSC survey area was divided into two geographic regions (the region north of Hudson Canyon to the Gulf of Maine [designated New England, NE] and the region south of Hudson Canyon to Cape Hatteras (designated Mid-Atlantic Bight [MAB]) and into four bottom depth zones (27–55 m, 56–110 m, 111–185 m, and 186–366 m [Fig. 1]). The 1–26 m depth zone was not sampled in NEFSC offshore surveys, but "inshore" strata were added to the survey in 1972.

For the spring and winter surveys, the combined effects of annual abundance (numbers of squid per standardized trawl haul), survey stratum, and time of day (night, 20:00–03:59; dawn and dusk, 04:00–07:59, 16:00–19:59; and day, 08:00–15:59), as described by Brodziak and Hendrickson (1999) for the autumn survey, were analyzed to determine adjustment factors for diel differences in log-transformed survey catches of prerecruit squid (≤80 mm dorsal mantle length [ML], the minimum size in commercial catches) and recruits (>80 mm ML). The derived factors were then used to adjust all survey catches to

[3] Lange, A. M. T. 1984. An assessment of the long-finned squid resource off the northeastern United States. Northeast Fisheries Science Center (NEFSC) Lab. Ref. Doc. 84-37, 24 p. [Available from NEFSC, 166 Water St. Woods Hole, MA 02543.]

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[5] Macy W. K. 1995. Recruitment of long-finned squid in New England (USA) waters. ICES CM 1995/K:35, 18 p. [Available from W. K. Macy, Graduate School of Oceanography, Univ. Rhode Island, South Ferry Road, Narragansett, RI 02882].

their daytime equivalent. The size groups (≤80 mm ML, >80 mm ML) were chosen to allow comparisons with results from previous studies (e.g. Lange, 1980; 1981; Lange and Sissenwine, 1983; Brodziak and Hendrickson, 1999; NEFC[1]; Lange and Sissenwine[2]; Lange[3]). Alternative analyses were performed for different size groups (≤50 mm ML, >50 mm ML and ≤100 mm ML, >100 mm ML) to assess the sensitivity of the results to the choice of size groups. The combined effects of geographic region (NE and MAB), depth zone, and year on survey catches were tested by using generalized linear models (GLM) to derive main effects and coefficients for each survey. Pairwise comparisons were tested by using a *t*-test with Bonferroni adjustments (Sokal and Rohlf, 1995) to compare specific regions, seasons, and depth zones. All tests were analyzed at the 5% significance level. Differences between seasons and regions were tested between autumn and spring surveys for the years 1968 to 1997, between autumn and winter for 1992 to 1997, and between spring and winter surveys from 1992 to 1998. Proportion of catches ≤50 mm ML were analyzed to evaluate the relative distribution of juvenile *L. pealeii*.

Biological analysis

Subsamples of 50–100 individuals were obtained from five different survey time series: NEFSC autumn (September–October 1997), winter (February 1998), and spring (March 1998), inshore Massachusetts (Howe[6]) (October 1997), and Connecticut (Johnson[7]) (Long Island Sound, May 1998). The samples were analyzed from each of five depth zones (1–26 m, 27–55 m, 56–100 m, 111–185 m, 186–366 m), within each of three geographic regions (Gulf of Maine [GOM]; Georges Bank–Southern New England, north of Hudson Canyon [SNE]; and Mid-Atlantic Bight, see above [MAB]). A fourth region, south of Cape Hatteras (SOH) was added later. Each sample comprised a nonrandom selection of lengths to represent the size range present in a tow. In total, 2156 individuals were subsampled from 53 survey tows. Sexes were determined and specimens were measured to enable the morphometric maturity analyses of Macy (1982); each individual squid was also weighed on a top-loading balance to 0.1 g. The morphometric method uses a suite of length measurements for female and male squid to determine maturity stage (measured on a scale of 1 to 4, where 1 is immature and 4 is fully mature). Opportunistic commercial samples from early winter (December 1998 and January 1999) were also analyzed (118 individuals) to bridge the temporal gap in survey coverage.

Data on dorsal mantle length (ML, mm) and total body mass (BM, g) for each maturity stage were used to estimate proportions for each maturity stage across the length and weight range. These proportions were used to determine the sizes at which squid of both sexes changed from one maturity stage to the next.

Maturity-at-length data were weighted by diurnally adjusted catch-at-length data for each depth zone and region to provide population-weighted maturity patterns, assuming that survey length distributions accurately represent relative proportions of population components. Catch-weighted data were analyzed to derive 1) the patterns of maturity for each sex at different times of the year; 2) estimates of proportions of each maturity stage sampled by survey; 3) mean length for each maturity stage of each survey; 4) mean length for each region of each survey; and 5) mean length for each depth stratum of each survey. A small proportion (8.4%) of survey catches ≤50 mm ML were not subsampled; these were assigned to the juvenile stage. Catches at larger sizes, which were not subsampled (6.8% of survey catches), were removed from the analysis because sex or maturity stage could not be assigned with any degree of certainty. Individual squid, or size classes of squid, were not weighed during NEFSC surveys; therefore the maturity data from the biological analysis could only be catch-weighted by length because length was measured on a random subsample of squid caught at each station in NEFSC surveys.

Results

Survey analysis

Patterns of diurnal distribution were different among seasons surveyed (Table 1). In winter surveys, from 1992 to 1998, prerecruit (i.e. ≤80 mm ML) catch was lower at night and during dawn and dusk than during daylight hours (65% and 81% of daytime catch, respectively). However, for recruits (i.e. >80 mm ML), catch was higher both at night and at dawn and dusk than during the day (131% and 115% of daytime catch respectively) in winter surveys. In autumn and spring surveys, from 1968 to 1998, both prerecruits and recruits showed a lower catch at night and during dawn and dusk than by day; recruits showed a lesser diurnal variation than prerecruits. Results from analyses with different size groups (≤50 mm ML, >50 mm ML and ≤100 mm ML, >100 mm ML) were very similar, suggesting that the interaction of size and time of day is gradual.

Catch rates varied significantly by season (Table 2). During winter and spring, survey catches were greater in the MAB by a factor of approximately four (Fig. 2). However, there was no significant difference in survey catches between geographic regions in autumn (Fig. 2). Pairwise comparisons showed that mean number-per-tow was significantly greater in autumn than in spring within both geographic regions and was greater in autumn than in winter in the NE. There were no significant differences between autumn and winter means in the MAB nor between spring and winter means in either the MAB or the NE.

Catch by depth, pooled over the MAB and NE, varied by season (Table 3). Pairwise comparisons of each depth for each season showed that winter and spring survey catches were lowest in the shallowest stratum (27–55 m), in-

[6] Howe, A. B. 1989. State of Massachusetts inshore bottom trawl survey. Atlantic States Marine Fisheries Commission (ASMFC) Spec. Rep. 17:33–38. [Available from ASMFC, 1444 Eye Street, N.W., sixth floor, Washington, DC 20005.]

[7] Johnson, M. 1994. State of Connecticut marine finfish trawl survey. Atlantic States Marine Fisheries Commission (ASMFC) Spec Rep. 35:24–26. [Available from ASMFC, 1444 Eye Street, N.W., sixth floor, Washington, DC 20005.]

Table 1

Relative catch rates for small (≤80 mm dorsal mantle length (ML)) and large (>80 mm ML) *Loligo pealeii* in three seasonal NEFSC bottom-trawl surveys, 1967–98, by time of day (in relation to catch rates during daytime).

	Winter		Spring		Autumn	
Time of day	≤80 mm	>80 mm	≤80 mm	>80 mm	≤80 mm	>80 mm
Night	0.65	1.30	0.51	0.72	0.09	0.34
Dawn and dusk	0.81	1.14	0.79	0.92	0.46	0.83
Day	1.00	1.00	1.00	1.00	1.00	1.00

Table 2

Results of generalized linear model (GLM) of survey mean numbers-per-tow by year, depth zone, and geographic region (df=degrees of freedom; SS=sum of squares; *F*=*F*-statistic; *P*=probability), for *Loligo pealeii* off the northeast United States, based on NEFSC bottom-trawl survey data, 1967–98.

Season and effect	df	Type III SS	Mean square	*F*	*P*
Winter					
year	6	42.51	7.09	2.71	0.0133
depth	3	339.62	113.21	43.36	0.0001
region	1	233.73	233.73	89.53	0.0001
Spring					
year	30	409.47	13.64	4.44	0.0001
depth	3	1696.53	565.51	183.79	0.0001
region	1	983.51	983.51	319.64	0.0001
Autumn					
year	30	557.85	18.59	5.17	0.0001
depth	3	1134.09	378.03	105.20	0.0001
region	1	9.12	9.12	2.54	0.1113

Table 3

Diurnally adjusted, mean numbers-per-tow of *Loligo pealeii* from the three annual NEFSC bottom-trawl surveys, 1967–98, by season.

	Depth zone (m)			
	27–55	56–110	111–185	186–366
Winter	42.9	103.1	215.5	30.3
Spring	42.6	90.7	342.5	91.9
Autumn	853.3	352.8	377.2	66.5

Table 4

Diurnally adjusted, mean numbers-per-tow of *Loligo pealeii* from the three annual NEFSC bottom-trawl surveys, 1967–98, by area (NE=north of Hudson Canyon to the Gulf of Maine; MAB=south of Hudson Canyon to Cape Hatteras.

	Depth zone (m)			
	27–55	56–110	111–185	186–366
Winter NE	6.0	38.9	160.4	28.7
Winter MAB	83.5	396.2	510.7	36.0
Spring NE	2.3	24.7	259.5	81.4
Spring MAB	86.8	392.3	787.3	129.7
Autumn NE	644.2	365.9	392.8	72.4
Autumn MAB	1082.5	293.1	293.7	45.5

creased to peak values in deeper strata (111–185 m, greater than 10 times the catches in the shallowest strata), and were low in the deepest stratum (>185 m). Conversely, autumn survey catches were highest in the shallowest stratum (27–55 m) and lowest in the deepest stratum (>185 m). These patterns were also generally significant within both geographic regions (Table 4).

In the pairwise comparisons of the winter and spring surveys, catches were significantly greater at 111–185 m than in other depth zones. In the 27–55 m depth zone, au-

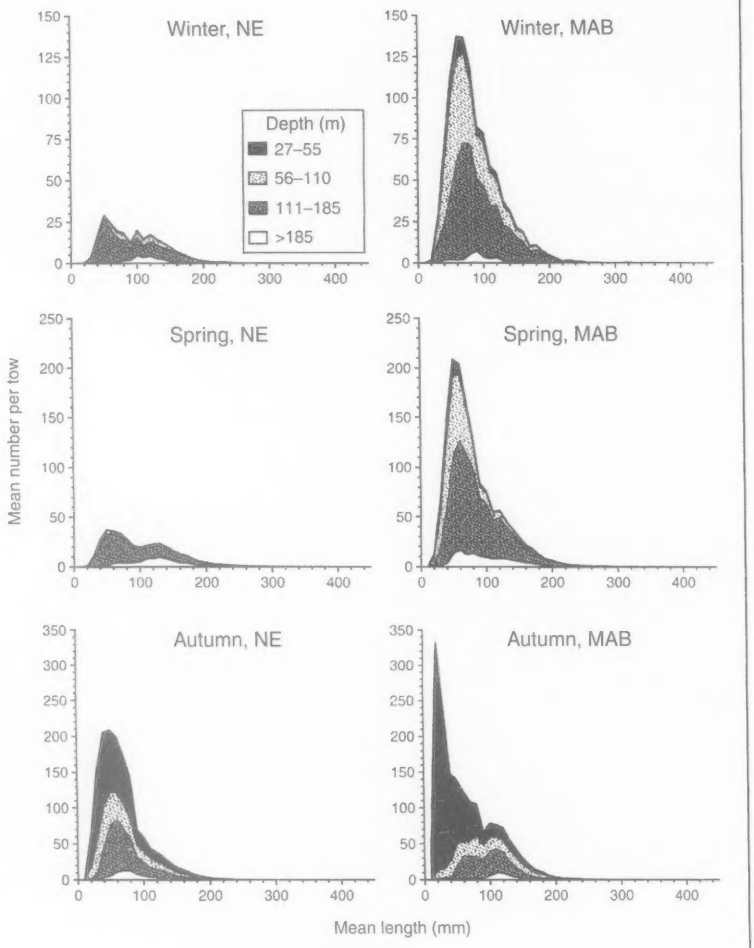

Figure 2

Diurnally adjusted mean numbers-per-tow of *Loligo pealeii*, by length class, from Northeast Fisheries Science Center, National Marine Fisheries Service, surveys, by season, region, and depth. NE = north of Hudson Canyon to Gulf of Maine; MAB = south of Hudson Canyon to Cape Hatteras.

tumn catches were considerably higher than in winter or spring. For all other depth zones and survey comparisons, the differences were not significant.

In the autumn survey, the proportion of small squid (≤50 mm ML) was highest at 27–55 m depths (over 50% of the sampled squid in that depth zone in the NE and almost 75% of the squid in that depth zone in the MAB, Table 5). Proportions of small squid at greater depths were considerably lower. These patterns show higher relative recruitment into the population in the shallow waters of the continental shelf in the autumn.

Similarly in the MAB during winter and spring, small squid form a higher proportion of squid sampled in the two shallowest depth zones than at greater depths. A higher percentage of small squid was present in spring than in winter, with over 60% of squid sampled in the MAB from 27–55 m being ≤50 mm ML. However, the highest proportion of small squid in the NE during winter and spring was at intermediate depths.

Biological analysis

The raw data of numbers sampled for each sex, length, and maturity stage are given in Table 6. For all seasons combined, the ML at 50% maturity during 1997–98 was approximately 200 mm ML for females and males (Table 7,

Table 5

The percentage of *Loligo pealeii* <50 mm ML in each depth zone, for each region and survey, and for the number of years for which these data were available (NE=north of Hudson Canyon to the Gulf of Maine; MAB=south of Hudson Canyon to Cape Hatteras).

	Winter		Spring		Autumn		Winter		Spring		Autumn	
Depth zone (m)	NE	(No. of years)	NE	(No. of years)	NE	(No. of years)	MAB	(No. of years)	MAB	(No. of years)	MAB	(No. of years)
27–55	3	6	17	20	51	31	33	7	64	30	73	31
56–110	11	7	40	31	19	31	27	7	48	31	27	31
111–185	27	7	24	31	31	31	14	7	22	31	9	31
186–366	7	3	2	31	14	30	10	3	14	31	2	31

Table 6

Numbers of *Loligo pealeii* measured, for each sex and maturity stage, from samples taken for biological analysis in 1997–99. Maturity was based on a four-stage scale for sexual maturity for each sex where 1 was immature and 4 was fully mature. ML = mantle length.

	Females					Males				
ML (mm)	Stage 1	Stage 2	Stage 3	Stage 4	Total ♀	Stage 1	Stage 2	Stage 3	Stage 4	Total ♂
30	1				1					
40	5				5	2				2
50	31	1			32	18				18
60	59	3	1		63	30	5		1	36
70	73	17	1		91	32	22	2	1	57
80	57	30	1	1	89	27	37	12	1	77
90	51	45	5		101	10	45	16	4	75
100	27	51	2	3	83	2	50	17	2	71
110	10	62	5	6	83	2	35	30	8	75
120	8	86	14	4	112	1	32	40	4	77
130	3	79	6	4	92		24	37	11	72
140	3	71	10	8	92		14	39	10	63
150	2	38	16	14	70		14	43	10	67
160		25	6	7	38		14	28	8	50
170		13	2	7	22		12	31	7	50
180		7	2	3	12		6	18	7	31
190		9	1	2	12		3	19	9	31
200		1		5	6			5	9	14
210		1	1	1	3		1	2	8	11
220			1	3	4		1	4	7	12
230							1		5	6
240							1	1	5	7
250							1	1	3	5
260									1	1
270				1	1				3	3
280									1	1
290									1	1
Total	330	539	74	69	1012	124	318	345	126	913

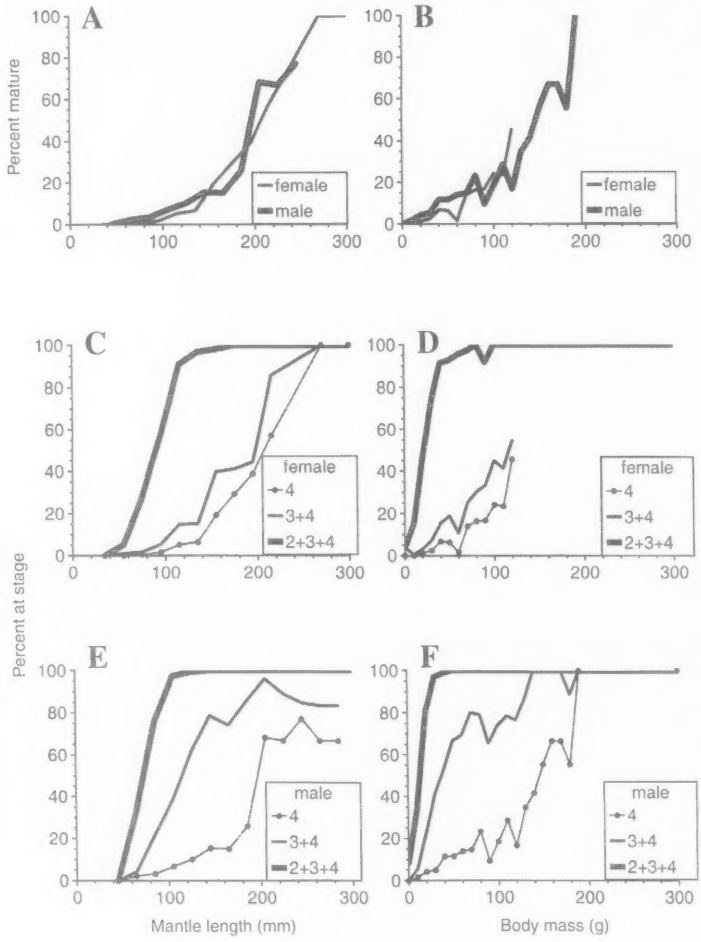

Figure 3

Percent mature of *Loligo pealeii* for dorsal mantle length (ML mm) (**A**) and wet body mass (BM g) (**B**). The percentage at each maturity stage is shown for female ML (**C**) and BM (**D**) and for male ML (**E**) and BM (**F**).

Table 7

Size at maturity for *Loligo pealeii* in mantle length (ML, mm) and body mass (BM, g), by sex. (—denotes a missing value).

	Female		Male	
Proportion mature	ML	BM	ML	BM
25%	166	111	184	113
50%	207	—	196	146
75%	238	—	241	184

Fig. 3, A and B). In terms of body mass, the size at 50% maturity for males was approximately 150 g, but, according to our samples, female maturity did not seem to be as closely associated with body mass (e.g. even squid in the heaviest size class were less than 50% mature).

In females, maturity stage 2 was reached at a relatively small size (Fig. 3, C and D). To reach stage 3 requires a considerable increase in length or body mass, whereas females in stage 4 are neither much longer, nor heavier than stage-3 females. Thus the transition from stage 3 to stage 4 (full maturity) takes place over a lesser period of somatic growth (and therefore possibly a shorter time period) than the transition from stage 2 to stage 3. In Macy's (1982) maturity stage notation, stage-3 females have no mature

Table 8

Diurnally adjusted, catch-weighted mean numbers-per-tow of *Loligo pealeii* sampled in each maturity stage. Maturity stages correspond to unsexed juveniles and a four-stage scale for sexual maturity for each sex where 1 was immature and 4 was fully mature (SOH: south of Cape Hatteras).

		Female				Male				
	Juvenile	Stage 1	Stage 2	Stage 3	Stage 4	Stage 1	Stage 2	Stage 3	Stage 4	Totals
Autumn	240.0	94.0	16.0	0.0	2.0	64.0	49.0	4.0	3.0	472.0
Winter	5.0	13.9	10.9	0.4	0.2	4.8	6.1	6.2	1.1	48.6
Spring plus SOH	26.3	12.7	10.0	2.3	1.4	5.4	5.0	5.0	2.4	70.5
Long Island Sound	436.0	0.0	52.0	378.0	176.0	161.0	0.0	196.0	144.0	1543.0
Commercial	0.0	5.0	155.0	0.0	0.0	8.0	198.0	331.0	15.0	712.0
Totals	707.3	125.6	243.9	380.7	179.6	243.2	258.1	542.2	165.5	2846.1

Table 9

Maturity patterns in *Loligo pealeii* (percentage of sample at each sex and stage derived from diurnally adjusted, catch-weighted mean numbers-per-tow. Maturity stages correspond to unsexed juveniles and a four stage scale for sexual maturity for each sex where 1 was immature and 4 was fully mature (SOH: south of Cape Hatteras).

		Female				Male			
	% juvenile	% stage 1	% stage 2	% stage 3	% stage 4	% stage 1	% stage 2	% stage 3	% stage 4
Autumn	50.7	20.0	3.4	0	0.5	13.6	10.3	0.9	0.6
Winter	10.3	28.7	22.4	0.7	0.4	9.8	12.5	12.7	2.2
Spring plus SOH	37.3	18.0	14.2	3.2	1.9	7.7	7.0	7.1	3.5
Long Island Sound	28.3	0	3.4	24.5	11.4	10.4	0	12.7	9.3
Commercial	0	0.7	21.8	0	0	1.1	27.8	46.5	2.1

oocytes (therefore they would not be considered to be close to maturity) and stage-4 females are fully mature.

In comparison, the transition of male squid (Fig. 3, E–F) from stage 2, to stage 3, to stage 4, seems more evenly spaced, with a more gradual development seen over the course of the maturation process. If anything, there seems to be a greater transition from stage 3 to stage 4, than from stage 2 to stage 3. The difference between stage-2 and stage-3 males is measured only as elongation of the testis in conjunction with a reduction in the ratio of mantle circumference to mantle length. In stage-4 males "elongate mature spermatophores are visible both in the Needham's sac and the penis." In subjective terms, stage 2 represents definitely immature, stage 3, maturing, and stage 4, fully mature males. Thus the rate at which full maturity is approached is very different between the sexes.

The raw data (numbers sampled in each size class, sex, and maturity stage) were then catch-weighted to be representative of the squid sampled in the different surveys and from commercial data. Catch-weighted proportions of female and male *L. pealeii* at each maturity stage are shown in Tables 8 and 9. In the autumn and spring surveys, and in the May Long Island Sound (LIS) samples, juvenile squid were the most abundant stage within the sampled population. In winter surveys the juveniles were one of the least abundant stages. Mature squid were never abundant in the NEFSC survey subsamples, nor in the inshore autumn (October) Massachusetts survey (combined with NEFSC data for autumn surveys). Most mature squid were seen in the LIS samples. In NEFSC surveys, the majority of both sexes were immature and stages 1 and 2. In LIS samples more squid were either stage 3 or 4 than immature. No mature females were observed in the commercial samples, although a small proportion of males were mature.

The catch-weighted mean ML for each maturity stage, by season, is given in Table 10. There was little difference between the size of juvenile squid between seasons. For both sexes, squid at stages 1, 2, and 3 were all longest in the autumn samples and shortest in the spring and LIS samples. Conversely, mature squid of both sexes (stage 4) were considerably larger in the spring than in autumn. In the LIS samples, mature female squid were the same size as in spring survey samples; mature male squid, on the other hand, were smaller than in the spring survey but larger than the autumn survey samples. Commercial samples showed a larger size for each maturity stage sampled.

Table 10

Mean dorsal mantle length (ML, mm) of *Loligo pealeii* for each sex and maturity stage (corresponding to unsexed juveniles and a four stage scale for sexual maturity for each sex where 1 was immature and 4 was fully mature), from diurnally adjusted, catch-weighted mean numbers-per-tow data (SOH: south of Cape Hatteras).

		Female				Male			
	Juvenile	Stage 1	Stage 2	Stage 3	Stage 4	Stage 1	Stage 2	Stage 3	Stage 4
Autumn	34	77	133		115	70	105	161	94
Winter	41	71	122	166	164	54	93	131	169
Spring plus SOH	37	58	90	122	139	61	83	114	143
Long Island Sound	47		90	79	138	70		83	109
Commercial		83	160			79	150	169	180

Table 11

Mean dorsal mantle length (ML, mm) and percentage of each sex for each sample of *Loligo pealeii* by depth stratum per survey. Derived from diurnally adjusted, catch-weighted tow data.

	Depth zone		Depth zone		Depth zone		Depth zone		Depth zone	
	<27 m	%	27–55 m	%	56–110 m	%	111–185 m	%	186–366 m	%
Autumn juvenile ML	32	73	29	72	47	58	48	5		0
Autumn female ML	67	13	87	13	95	25	92	21	123	68
Autumn male ML	67	14	105	15	111	17	80	74	118	27
Winter juvenile ML			42	10	39	4	39	5	46	5
Winter female ML			100	68	84	63	97	47	111	47
Winter male ML			105	22	93	33	97	48	131	48
Spring juvenile ML	35	42	43	3	37	54	40	3	43	1
Spring female ML	60	32	113	61	78	26	100	47	123	48
Spring male ML	59	25	129	36	90	18	104	49	136	51
Long Island Sound juvenile ML	47	28								
Long Island Sound female ML	97	39								
Long Island Sound male ML	86	33								
Commercial female ML							158	23		
Commercial male ML							161	78		

The distribution of the catch-weighted mean ML, by sex, by depth zone, for each season separately is shown in Table 11. For juvenile *L. pealeii*, in autumn, at 1–55 m depth, there was little difference in size at depth. In the 56–110 m depth zone, juveniles in autumn were considerably larger than at shallower depths. In winter, there was evidence for a slight increase in the size of juveniles with increasing depth. In spring survey samples, juveniles were similar in size across the depth range sampled.

Female and male *L. pealeii* were generally smaller in the shallowest depth zone (1–26 m, only sampled in autumn and spring surveys), and much larger at depths greater than 185 m, for each survey. There was no clear pattern for intermediate depths. In autumn surveys, squid were generally smaller at 27–55 m depth than in deeper water. In winter and spring, however, squid at this depth were longer than at 56–185 m. The LIS samples showed larger mean sizes for each group at <27 m depth than in autumn and spring samples.

In the autumn survey, squid of all maturity stages (except juveniles) were generally largest in the south (MAB) and smallest in the north (SNE and GOM, Table 12). Some of this distribution may have been an artifact of the sampling design because no squid were sampled in the MAB region in the 1–26 m depth zone, whereas this zone was sampled in the SNE, and was the only zone for which data were available for the GOM region.

In the winter survey, the general pattern was the reverse of that seen in the autumn. In this survey squid were generally smaller in the south (MAB) than in the

Table 12

Mean dorsal mantle length (ML, mm) by sex and maturity stage (corresponding to unsexed juveniles and a four-stage scale for sexual maturity for each sex, where 1 was immature and 4 was fully mature)of *Loligo pealeii* by region per survey. Derived from diurnally adjusted, catch-weighted mean numbers-per-tow data. MAB = Mid-Atlantic Bight; SNE = Georges Bank–Southern New England, north of Hudson Canyon; GOM = Gulf of Mexico; SOH = South of Cape Hatteras.

		Female				Male			
	Juvenile	Stage 1	Stage 2	Stage 3	Stage 4	Stage 1	Stage 2	Stage 3	Stage 4
Autumn MAB	23	98	132		162	69	120	172	170
Autumn SNE	38	71	130		85	69	102	147	96
Autumn GOM	33	68				65	69		71
Winter MAB	42	67	116	186	180	59	94	128	151
Winter SNE	50	80	127	148	159	52	94	134	171
Spring MAB	37	62	93	127	154	66	82	110	150
Spring SNE	41	51	95	132	151	54	88	125	183
Spring SOH		56	70	77	137	54	81	98	162
Long Island SNE	47		90	79	138	70		83	109
Commercial SNE		83	160			79	150	169	180

north (SNE only, no GOM samples were taken in the winter survey). The exception in winter were the few stage-3 and stage-4 females sampled.

In the spring survey, the same pattern as in the winter survey was observed; squid in the south were smaller than in the north. In the spring survey, samples available from south of Cape Hatteras (the limit of the MAB samples) followed the same trend because the observed mean sizes were smaller than the MAB samples. The exception to this were maturity-stage-1 squid.

Discussion

Survey analysis

The high proportion of small squid (≤50 mm ML) in the winter and spring surveys corroborated the occurrence of an early winter hatching event, documented from age data determined by squid statolith analysis (Brodziak and Macy, 1996; Macy[5]).

Mean numbers-per-tow of juvenile squid in the MAB were considerably higher than in the NE in all seasons surveyed. Recruitment of squid into the population was highest in autumn, but juvenile squid were distributed more widely over the continental shelf in the spring. Perhaps the MAB component of the *L. pealeii* stock was larger because it is more stable—a result of the higher proportion of squid recruited into the area each winter, spring, and autumn.

Murawski (1993) inferred a centering of the population in the MAB subject to the issue that portions of the stock are outside the area of the NEFSC surveys. Our data suggested that the area south of Cape Hatteras may play an important role in reproductive dynamics and recruitment to the population, suggesting that a considerable portion of the stock is south of the surveyed area, particularly during winter and spring. South of Cape Hatteras a second loliginid species, *L. plei*, is abundant (Roper et al., 1984). In our study, all *Loligo* specimens were examined carefully to ensure that only *L. pealeii* were measured and included in the biological analyses.

Diel differences in catches of *L. pealeii* have been observed in a number of studies (Summers, 1969; Serchuk and Rathjen, 1974; Roper and Young, 1975; Sissenwine and Bowman, 1978; Lange and Sissenwine, 1983; Lange and Waring, 1992), where catches were consistently higher in daytime than at night. To account for diel effects on minimum swept-area estimates of *L. pealeii* biomass and stock size, nighttime catches were adjusted to daytime equivalents by using the diel correction factors of Lange and Sissenwine (1983). However, these correction factors were not size specific. Brodziak and Hendrickson (1999) applied size-specific diel correction factors to squid from the autumn survey (1967–94), splitting the data into prerecruits (≤80 mm ML) and recruits (>80 mm ML). In the autumn surveys the nighttime catch of prerecruits was only 8.7% of the daytime catch. The nighttime catch of recruits was 34% of the daytime catch. These differences were attributed to the different feeding behavior of juvenile and adult squid, in that juvenile squid might need to undertake more vertical migrations at night to meet their higher metabolic requirements. In our present study, prerecruit nighttime catch differed to a lesser degree from the daytime catch in the winter and spring (65% in the winter surveys, and 51% in the spring surveys) than in the autumn. In the winter surveys, nighttime catches of recruits exceeded daytime catches by 31%. In spring, nighttime tows showed a lower catch of recruits, 72% of daytime values, than in winter. Patterns of diel differences reported in another study by Lange and Waring (1992) for spring catches were similar to those in our study. Their

reported autumn catches (Lange and Waring, 1992) were higher at night than in our study, but still lower than daytime catches.

The behavior of squid at both prerecruit and recruit sizes therefore appears to be different in the winter and spring than in the autumn. The prerecruit nighttime catch in winter and spring was half, or more than half of daytime catches, as opposed to 9% in autumn. For recruits, there was an even greater difference among seasons. In winter, almost 1.5 times as many squid were caught at night, than by day. In spring the nighttime catch was 72% of the daytime catch, twice the proportion of the autumn catch. Vovk (1978; 1985) and Maurer and Bowman (1985) have documented large changes in the diet of squid in different seasons, relating these changes in feeding activity and dietary preference to changes in the size composition of the squid population, movements of squid in search of food concentrations, seasonal abundance of prey, and environmental conditions that affect both prey and predator. Vovk (1985) noted that in autumn *L. pealeii* are daytime predators and do not feed extensively at night when they occur at shallow depths. In autumn, squid are more abundant near the seafloor by day (Brodziak and Hendrickson, 1999). Vovk (1985) also noted that feeding activity was generally low from December to April and related this to possible prey abundance. Perhaps the different diel behavior patterns of *L. pealeii* in winter and spring, when they appear to be more available to capture by bottom-trawls, are related to a lower prey abundance and a requirement for more time to be spent searching for prey. Some of these differences might be temperature related as well. In the autumn, with strong vertical stratification of the water column, there may be some physiological benefit for squid to move off the bottom at night into warmer waters. In winter and spring when there is no vertical stratification, no advantage is conferred by a strong diel migration as seen in the autumn.

Comparisons in performance and catchability of the two trawl nets used in the spring and autumn surveys (Yankee 36 and Yankee 41) have been conducted (Sissenwine and Bowman, 1978), but any differences in catchability were confounded by diel and vessel differences. In our study, we corrected for diel differences, and vessel differences were not found to be significant (NEFSC[8]).

Squid catches are more abundant in the autumn surveys than in winter and spring (Serchuk and Rathjen, 1974; Lange and Waring, 1992; Lange and Sissenwine[2]). This difference may be related to the recruitment of large numbers of small squid, present in shallow water, in autumn. Temperature, however, is a major factor limiting distribution. In winter and spring much of the continental shelf water is below the preferred temperature minimum for the species (ca. 8°C) (Summers, 1969; Serchuk and Rathjen, 1974; Murawski, 1993); therefore squid are apparently less abundant than in the autumn surveys when temperature is not a limiting factor. The greatest differences between autumn and spring or winter surveys are most apparent in the NE, where a large portion of the stock may be outside the surveyed area owing to temperature limits (e.g. off the shelf or south of Cape Hatteras). In the MAB there are few differences in catches between spring and autumn at depths deeper than 27–55 m. Spring numbers are higher than autumn numbers from 111 to 185 m. The patterns between autumn and winter catches are similar to each other at that depth. Catches are always lower in winter than in autumn, but the differences are only significant from 27–110 m depth.

In winter and spring surveys, catches were highest from 111 to 185 m, both in the NE and the MAB. Catches were higher, in both surveys, in the MAB than in the NE. These patterns also were observed for *L. pealeii* in survey analyses from 1967 to 1971 (Summers, 1969; Serchuk and Rathjen, 1974), from 1970 to 1977 (Lange, 1980), and from 1975 to 1986 (Lange and Waring, 1992). This finding may imply that geographic distribution is relatively stable for *L. pealeii*, during February and March, at least within the areas surveyed. In autumn surveys, Serchuk and Rathjen (1974), Lange (1980), and Lange and Waring (1992) also reported highest catches in the MAB. However, Serchuk and Rathjen (1974) showed a relatively higher abundance of squid taken from 56–110 m depth than that observed in our study, where mean numbers per tow in the depth zone 27–55 m were greater than three times higher than those in the zones 56–110 m and 111–185 m. The difference between the 27–55 m zone and deeper strata was less noticeable in the NE, although mean numbers-per-tow were almost twice as high in the 27–55 m zone. The differences may result from diurnal adjustments, or from the inclusion of more years of data in the survey database. Lange (1980) found mean numbers-per-tow in the NE autumn to be highest from 111 to 185 m depths.

Biological analysis

We found that squid mature at greater lengths than previously reported for *L. pealeii* (NEFSC[8]). Figure 3 (C–F) shows that using stage 3 or greater to indicate maturity may be an adequate proxy for females. For example, the size at which 50% of females are mature is 198 mm with stages 3 and 4, and 207 mm with only stage 4 (Fig. 3C). Such a proxy may be valuable for samples with few observations of stage-4 females (e.g. the body mass at 50% maturity is 120 g with stages 3 and 4 [Fig. 3D]).

For males, however, the size difference between stage 3 and stage 4 is considerable, and substantial somatic growth is required to develop from stage 3 to stage 4. Combining the two maturity stages in males is therefore unsupported biologically, and the combined data would underestimate size at 50% maturity.

That mature squid are largest in winter and smallest in autumn samples (and intermediate in size in the early [NEFSC] and late [LIS] spring) has been noted previously (Summers, 1971; Lange, 1980; Macy, 1980). Prior to the availability of age data for the species, the size differences at maturity were ascribed to different year class-

[8] NEFSC (Northeast Fisheries Science Center). 1996. Report of the 21st Northeast Regional Stock Assessment Workshop (SAW 21). Center Reference Document 90-05, 200 p. [Available from NEFSC, 166 Water St., Woods Hole, MA 02543.]

es (Summers, 1971; Lange, 1980; Macy 1980). The observation that immature squid are larger in autumn than in winter and spring was documented by Lange (1980) but not interpreted. Some of this variability might be explained as a function of temperature. If *L. pealeii* have a life-span of 9–12 months (Brodziak and Macy, 1996), then females that are mature in September–October samples would have hatched between November and January. Females that are mature in March would have hatched around May or June. Brodziak and Macy (1996) showed that squid hatched between November and April had a lower growth rate than those that hatched between May and October. Recent laboratory studies on small *L. pealeii* have indicated that squid grow significantly faster at higher temperatures (Hatfield et al., 2001), in accord with results described for other cephalopod species (*Octopus bimaculoides*—Forsythe and Hanlon, 1988; *L. forbesi*—Forsythe and Hanlon, 1989; *Sepia officinalis*—Forsythe et al., 1994). These laboratory studies also found that the effect of temperature on growth is most pronounced during the early life cycle of these cephalopods, nominally the first three months. If temperatures experienced by *L. pealeii* hatching in May and June are warmer than temperatures experienced by squid hatching from November to January, then the growth potential will be lower for winter-hatching squid (seen as mature squid in autumn surveys), resulting in the observed lower size at maturity in autumn versus winter and spring. The same phenomenon would explain the size differences of immature squid among seasons. The large immature squid caught in the autumn survey are probably the same squid that become the large, mature squid in the winter, spring, and LIS samples. The small immature squid in the spring are probably those squid which become the small mature squid seen in autumn survey samples. If the winter-hatching squid are from southern spawning events, then the temperature difference between winter-spawned and summer-spawned squid may not be very large. However, age data for *L. pealeii* show that growth rates are generally slower for winter hatched squid. Also, growth studies on *L. forbesi* have shown that a temperature difference of just 1°C can change growth rates of squid by 2% body weight/day and produce a threefold difference in weight at 90 days after hatching (Forsythe and Hanlon, 1989).

The high numbers of juvenile squid in the autumn survey were from protracted spawning in inshore waters some 4–5 months previously (documented since Verrill [1882] first reported inshore spawning). The high proportion in spring therefore reflects a period of spawning, possibly also some 4–5 months earlier, around September or October of the previous year. Juvenile squid in winter and spring survey samples denote the presence of a hatching component other than the main inshore autumn component. The high proportion observed in LIS (May) samples probably reflects an extended winter–spring spawning period because squid of the size found in Long Island Sound in May could not have been the result of that season's inshore spawning. The inshore spawning season does not usually begin until late April and incubation time may require up to 4 weeks at the temperatures at that time of year (27 days at 12°C, McMahon and Summers, 1971). Brodziak and Macy (1996) showed a pattern of year-round hatching, which is consistent with the patterns suggested by our data.

Summers (1969), Serchuk and Rathjen (1974), and Brodziak and Hendrickson (1999) all reported an increase in size of *L. pealeii* with increasing depth. We found the smallest squid in the shallowest water and the largest squid in the deepest water, confirming that nearshore waters of the continental shelf are a preferred habitat for juvenile *L. pealeii* during the autumn (as described by Brodziak and Hendrickson [1999]). The pattern of ontogenetic descent exhibited by other loliginid species (*L. vulgaris*—Worms, 1983; *L. gahi*—Hatfield et al., 1990; *L. vulgaris reynaudii*—Augustyn et al., 1992) is consistent in *L. pealeii*, but less marked at intermediate depths.

In winter and spring, mean length is generally higher in the NE and lower in the MAB. In autumn, mean length is generally lower in the NE and higher in the MAB. Lange (1980) showed a similar pattern for immature females from the autumn survey. Males, however, showed the opposite pattern. Lange's (1980) winter and spring survey data showed the same pattern as our study for immature females and all males, except the fully mature squid.

Commercial samples from early winter (December and January) contained no mature female squid that might produce the winter hatching component evident from age data and aggregated survey length-frequency distributions. Egg masses are only found consistently in one small offshore area (off Chesapeake Bay) by commercial fishermen in the early winter (see Fig. 4). However, the commercial samples were from the southern edge of Georges Bank, and the survey data suggest that the winter recruitment originates from the southern part of the MAB. The scarcity of mature squid in NEFSC survey samples suggests that sampling did not occur consistently in the right areas or seasons to identify major spawning peaks. Whitaker (1978) documented that about 40% of males were fully mature in January and February in the region south of Cape Hatteras, off the coast of South Carolina. There was a large proportion of mature squid in samples from March and April, with 74% of females and 56% of males fully mature. There is evidence for both spawning and hatching in the SNE from March to April; as in 1999, egg masses were caught incidentally from northeast of Hudson Canyon and up towards the southern flank of Georges Bank, at depths of about 200 m, from mid-March to late April (Stommell[9]). In the 1998 Massachusetts spring survey, in mid-May, a high abundance of small squid, about 30 mm ML, were caught south of Martha's Vineyard, at depths of <27 m (senior author, personal obs.). These observations suggest that spawning is probably protracted, from early to late winter, and early winter spawning is more dominant in the southern end of the U.S. continental shelf. Thus, the available fishery-dependent samples may not be indicative of the population. The information on age and maturity in Brodziak and Macy (1996) was derived from

[9] Stommell, M. 1999. Personal. commun. FV *Nobska*, Woods Hole, MA 02543.

data collected from the winter fishery, most of which occurs north of the MAB region. A more structured design is required to address some of these issues. The entire size and maturity stage range needs to be sampled across the geographic range of each survey and these data should be augmented with opportunistic sampling outside the area or time frame in which the surveys are carried out.

In summary, results from these two studies complement each other to reveal patterns of reproductive dynamics for *L. pealeii* that have been suggested previously in other studies but that have never thoroughly been investigated. The high frequency of small squid present in spring survey catches indicates that winter spawning is indeed an important component of reproduction for the population, and biological analyses suggest that this winter spawning occurs primarily south of Cape Hatteras, rather than in the vicinity of the offshore submarine canyons along the edge of the northeastern U.S. continental shelf, from Hudson Canyon up to Georges Bank.

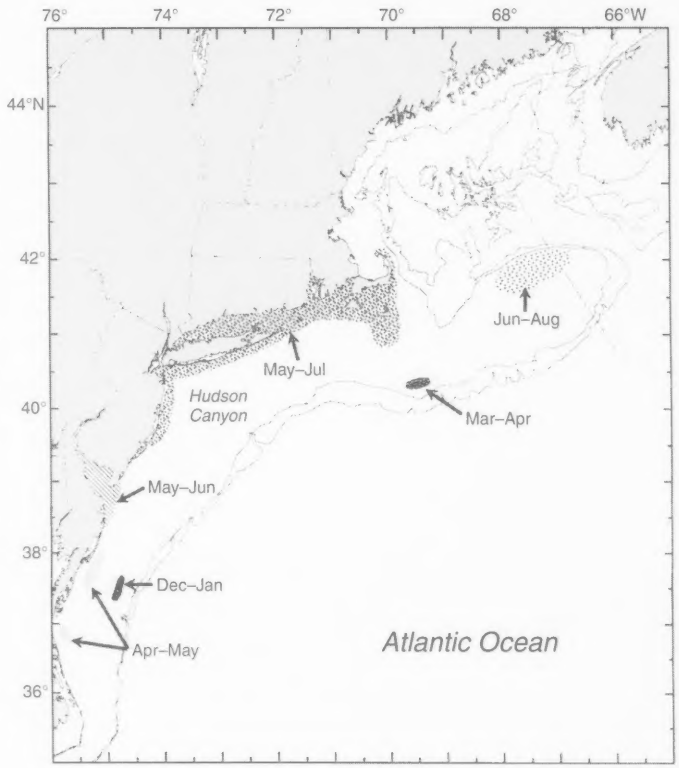

Figure 4

Persistent spawning areas and seasons for *Loligo pealeii*, as indicated from incidental catches of eggs in commercial squid trawls.

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Age and size composition, growth rate, reproductive biology, and habitats of the West Australian dhufish (*Glaucosoma hebraicum*) and their relevance to the management of this species

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Abstract–Samples of the commercially and recreationally important West Australian dhufish (*Glaucosoma hebraicum*) were obtained from the lower west coast of Australia by a variety of methods. Fish <300 mm TL were caught over flat, hard substrata and low-lying limestone reefs, whereas larger fish were caught over larger limestone and coral reef formations. Maximum total lengths, weights, and ages were 981 mm, 15.3 kg, and 39 years, respectively, for females and 1120 mm, 23.2 kg, and 41 years, respectively, for males. The von Bertalanffy growth curves for females and males were significantly different. The values for L_∞, k, and t_0 in the von Bertalanffy growth equations were 929 mm, 0.111/year, and –0.141 years, respectively, for females, and 1025 mm, 0.111/year, and –0.052 years, respectively, for males. Preliminary estimates of total mortality indicated that *G. hebraicum* is now subjected to a level of fishing pressure that must be of concern to fishery managers. *Glaucosoma hebraicum*, which spawns between November and April and predominantly between December and March, breeds at a wide range of depths and is a multiple spawner. The L_{50}'s for females and males at first maturity, i.e. 301 and 320 mm, respectively, were attained by about the end of the third year of life and are well below the minimum legal length (MLL) of 500 mm. Because females and males did not reach the MLL until the end of their seventh and sixth years of life, respectively, they would have had, on average, the opportunity of spawning during four and three spawning seasons, respectively, before they reached the MLL. However, because *G. hebraicum* caught in water depths >40 m typically die upon release, a MLL is of limited use for conserving this species. Alternative approaches, such as restricting fishing activity in highly fished areas, reducing daily bag limits for recreational fishermen, introducing quotas or revising specific details of certain commercial hand-line licences (or doing both) are more likely to provide effective conservation measures.

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The West Australian dhufish (*Glaucosoma hebraicum*), also known as the Westralian jewfish (McKay, 1997), is one of the most commercially valuable and recreationally sought after finfish in Western Australia (Sudmeyer et al.[1]). This species is confined to southwestern Australia, where its distribution ranges southwards from Shark Bay at 26°00′S, 113°00′E down the west coast and then eastwards along the south coast to the Recherche Archipelago at 34°10′S, 122°15′E (Hutchins and Thompson, 1995). *Glaucosoma hebraicum* is one of four members of the monogeneric family Glaucosomatidae, which also includes the pearl perch (*Glaucosoma scapulare*) that is fished commercially and recreationally in eastern Australia (McKay, 1997).

Despite the high quality of the flesh of *Glaucosoma* species and the commercial and recreational importance of *G. hebraicum* in particular, there are no refereed papers on the biology of any species in this genus. Furthermore, the results of undergraduate studies on the biology of *G. hebraicum*, which were collated by Sudmeyer et al.,[1] included estimates of age that were based on the number of growth zones in whole otoliths, an approach that would almost certainly have underestimated the age of many older fish (see "Results" section).

Numerous commercial and recreational fishermen report that they now fish much farther offshore in order to obtain catches of dhufish comparable with those they had previously been able to obtain from nearer the coast. This consistent circumstantial evidence strongly suggests that the abundance of *G. hebraicum* in more inshore waters has declined in recent years and that this is particularly the case in areas near the city of Perth where this species has been targeted by recreational fishing crews. The indications that the abundance of dhufish in nearshore waters was declining led the Australian Fisheries Research and Development Corporation to fund the current study, with a view to producing biological data for managing *G. hebraicum*.

During the present study, we first determined whether the otoliths of *G. hebraicum* had to be sectioned to detect all of their opaque zones and we then validated that these opaque zones are formed annually and could thus be used to age this species. As accurate estimates of the age of a fish are dependent on a reliable birth date, the trends exhibited by reproductive variables were used to estimate the duration of the spawning period and, in particular, when spawning activity peaked. The age of each fish was then determined and the resulting length-at-age

[1] Sudmeyer, J. E., D. A. Hancock, and R. C. J. Lenanton. 1992. Synopsis of Westralian jewfish (*Glaucosoma hebraicum*) (Richardson, 1845) (Pisces: Glaucosomatidae). Fisheries Research Report 96, Western Australian Marine Research Laboratory, Fisheries Western Australia, PO Box 20, North Beach 6020, Western Australia.

data employed to determine the age compositions and growth rates of female and male *G. hebraicum*. The reproductive variables were also used to help ascertain where *G. hebraicum* spawns and whether this species is a multiple spawner *sensu* deVlaming (1983), i.e. whether individual females release eggs on more than one occasion in a spawning season. The lengths of both sexes at first maturity were calculated to determine whether they lay below the minimum legal length (MLL) of 500 mm and were thus appropriate for helping to conserve this species. The ages at which females and males mature were also determined in order to elucidate whether fish might spawn in one or more spawning seasons before they attain the MLL. Attempts were also made to ascertain the types of habitat occupied by *G. hebraicum* at different stages during its life cycle and to obtain preliminary mortality estimates which could be used as an indicator of whether this species is being lightly or heavily fished. Finally, the data collected during this study were used to discuss ways in which the fishery for *G. hebraicum* might be managed most appropriately in the future.

Materials and methods

Glaucosoma hebraicum, that were less than the MLL of 500 mm total length (TL), were collected between May 1996 and June 1999 by commercial trawls, hand-lines, and a recreational spear diver under a research collection permit issued by Fisheries Western Australia—the government agency responsible for managing the fishery for this species. Filleted carcasses of *G. hebraicum* ≥500 mm TL, together with their gonads, were obtained monthly between May 1996 and April 1998 from commercial fish-processing plants and weigh-ins at local recreational fishing club competitions. These fish had been caught by commercial or recreational rod and hand-lines along the lower west coast of Australia between Mandurah (32°32′S) and the Houtman Abroholos (28°35′S), i.e. within that part of the distribution of *G. hebraicum* where this species is considered to be most abundant and is most heavily fished.

The total length of each fish was measured to the nearest 1 mm and the weight of each fish <500 mm was weighed to the nearest 1 g. The weights of 334 females and 442 males ≥500 mm TL were weighed to the nearest 10 g prior to filleting. The relationship between total length (L) in mm and total wet weight (W) in g of each sex was

$$\text{Females} \quad \log W = \log 0.0000417 + 2.859 \log L \quad (n=486,\ r^2=0.995)$$

$$\text{Males} \quad \log W = \log 0.0000322 + 2.898 \log L \quad (n=572,\ r^2=0.995).$$

These relationships were then used to estimate the weights of the female and male fish that had been filleted but not weighed. Note that all of the logarithm values recorded in this paper are natural logarithms.

On several occasions, a video camera, attached by cable to a television monitor and video recorder, was lowered over the substrata during commerical hand-line fishing for dhufish. Video footage of the substrate over which dhufish were caught was later examined to determine the types of habitat occupied by this species.

Age determination

The two sagittal otoliths of each fish were removed, cleaned, dried, and then stored in paper envelopes. All sagittal otoliths were sectioned, except for those which, when placed in methyl salicylate and examined microscopically under reflected light against a black background, could clearly be seen to possess either no opaque zones or only a single opaque zone. However, because the opaque zones in the whole otoliths of large fish were so numerous and closely spaced that they were often difficult to distinguish from one another and because previous estimates of the age of dhufish were based on counts of opaque zones in whole otoliths (Sudmeyer et al.[1]), the number of opaque zones visible in 100 otoliths, obtained from a wide size range of fish, were compared prior to and after sectioning to ascertain whether sectioning increased one's ability to detect the opaque zones.

For sectioning, the otoliths were mounted in clear epoxy resin and cut into 500 µm sections with a low-speed diamond saw (Buehler). The sections were cleaned and mounted on slides with DePX mounting medium and examined under reflected light with a dissecting microscope attached to a video camera (Panasonic WV-CD20). The image was analyzed by using the computer imaging package Optimas 5 (Optimas, 1995). The number of opaque zones in each otolith was always counted twice and on different days and without knowledge of either the date of capture or the size of the fish from which the otolith came, and also, in those cases where the two counts differed, on a third occasion. Although the number of times that a third count did not agree with either of the two previous counts was negligible for otoliths with less than 15 opaque zones, such disagreement increased to ca. 10% for otoliths with 15–25 opaque zones and ca. 30% for those with more than 25 opaque zones. When a third count was necessary and was not the same as either of the two previous counts, further counts were made until successive counts did not differ by more than two opaque zones. On such occasions, the final count was recorded.

An independent reader counted the number of opaque zones on 110 otoliths from a wide size range of fish. Eighty four percent of the counts of the number of opaque zones made by this independent reader were the same as those of the senior author for 50 sectioned otoliths that had been judged by the senior author to have up to 10 such zones and, in those cases where there were discrepancies, the differences were never more than one opaque zone. Eighty percent of the counts made by the independent reader of the number of opaque zones on 50 sectioned otoliths recorded as possessing between 11 and 25 such zones by the senior author were the same or differed by only one from those of the senior author and, where there were discrepancies, these rarely exceeded three opaque zones. In the case of ten otoliths with >25 opaque zones, the maximum dis-

crepancy between the counts recorded by the independent reader and the senior author was five. After consultation, it was agreed that, in many of the cases where the counts differed by one opaque zone, the independent reader had failed to discern the outermost opaque zone at the periphery of the otoliths. Moreover, the extent of any discrepancy between the counts of the independent reader and the senior author declined if the independent reader continued to recount the number of opaque zones on the otoliths.

Validation that the opaque zones in the otoliths of *G. hebraicum* are formed annually was carried out by analyzing the trends exhibited throughout the year by the marginal increments on whole otoliths, when only one opaque zone was present, and on sectioned otoliths when two or more opaque zones were present. For this purpose, the marginal increment on each otolith, i.e. the distance between the outer edge of the single or outermost opaque zone and the edge of the otolith, was expressed either as a proportion of the distance between the primordium and the outer edge of the opaque zone, when only one opaque zone was present, or as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more opaque zones were present. Each of the above requisite distances was measured perpendicular to the opaque zone(s) and without knowledge of the date of capture of the fish and was recorded to the nearest 0.01 mm by using Optimas 5. The values for the marginal increments were separated into groups according to the number of opaque zones on the otoliths, i.e. 1, 2–5, 6–8, 9–11 etc., after which the values for each of those groups in each corresponding month of the year between May 1996 and April 1998 were pooled.

Von Bertalanffy growth equations

The time when spawning peaked was estimated from the trends exhibited throughout the year by gonadosomatic indices, gonadal maturity stages, and pattern of oocyte development. This time was considered to correspond to the birth date of *G. hebraicum* and could thus be used, in combination with the number of opaque zones on the otolith and the time when the annulus becomes delineated on the otolith, to determine the age of individual fish on their date of capture. Because the sex of fish <150 mm could not be determined, the lengths-at-age of these small fish were randomly allocated in equal numbers to the data sets for female and male fish used for constructing the growth curves.

Assumptions are made concerning the distribution of errors when fitting von Bertalanffy growth curves to length-at-age data. Kimura (1980) discussed the implications of the following three assumptions, namely that 1) the individual lengths-at-age have a constant variance, 2) the mean lengths-at-age have a constant variance and 3) the variance of the lengths-at-age is dependent on age. The assumption most frequently adopted in growth studies is that the individual lengths-at-age have a constant variance. As discussed by Kimura (1980), different assumptions regarding the error variance require modifications to the objective function to ensure that the parameters are estimated accurately and that any comparisons between growth curves, that are based on the likelihood ratio, are appropriate.

A von Bertalanffy growth equation was fitted to the lengths-at-age of female and male fish with the traditional assumptions that the lengths-at-age are normally distributed around the values predicted from the growth equation and that the variance of this distribution is constant for each sex over all ages. However, visual examination of the residuals for each curve suggested that it was not appropriate to make the latter assumption. Further study showed that the variance of the residuals is approximately proportional to the age of the fish, as above in assumption 3 of Kimura (1980). Thus, the von Bertalanffy growth equation was fitted to the length-at-age data for each sex by using the assumption that the residuals were normally distributed, where the variance of this distribution was proportional to age but dependent on sex. That is,

$$\hat{L}_j = L_\infty\left\{1-\exp\left[-k(t_j - t_0)\right]\right\}$$

$$\text{and } L_j = \hat{L}_j + \varepsilon_j,$$

where, for each sex, L_j = the observed length at age;
$\hat{L}_j$ = the estimated length-at-age;
t_j = the age; and
ε_j = the error associated with the jth fish.

For the growth curves for females and males, L_∞ is the mean asymptotic length predicted by the equation, k is the growth coefficient, and t_0 is the hypothetical age at which fish would have zero length if growth had followed that predicted by the equation. The errors are assumed to be normally distributed, such that $\varepsilon_j \sim N(0, c_s t_j)$, where c_s is the constant of proportionality between the variance of the residuals and age for fish of sex s. The growth equations were fitted to the observed length-at-age data for both sexes by maximizing the log-likelihood of the data. The log-likelihood for the combination of male and female fish, λ, may be written as

$$\lambda = \lambda_M + \lambda_F,$$

where λ_s = the log-likelihood associated with females or males and may be calculated as

$$\lambda_s = -\frac{n_s}{2}\log(2\pi) - \frac{1}{2}\sum_{j=1}^{n_s}\log(c_s t_j) - \frac{1}{2c_s}\sum_{j=1}^{n_s}\left\{\frac{(L_j - \hat{L}_j)^2}{t_j}\right\},$$

and n_s = the number of fish of that sex in the length-at-age data.

The maximum likelihood estimate of c_s for each sex is given by

$$c_s = \frac{1}{n_s}\sum_{j=1}^{n_s}\left\{\frac{(L_j - \hat{L}_j)^2}{t_j}\right\}.$$

The SOLVER routine in Microsoft EXCEL (Microsoft Corp., 2000) was used to estimate the parameters that

would maximize the log-likelihood function, by fitting the equations to the combined set of length-at–age data for both females and males.

The growth curves for the fish of each sex were compared following the likelihood ratio method described by Kimura (1980) and Cerrato (1990). The test of the likelihood ratio, Λ, that was applied was to reject the null hypothesis Ω (that there was no difference between the curves) at the α level of significance when

$$\Lambda^{-2/n} > \left(1 + \frac{q}{f_M + f_F} F^{\alpha}_{qf_M+f_F}\right),$$

where $\Lambda = \left(\frac{\hat{\sigma}^2_{M\omega}}{\hat{\sigma}^2_{M\Omega}}\right)^{-n_M/2} \left(\frac{\hat{\sigma}^2_{F\omega}}{\hat{\sigma}^2_{F\Omega}}\right)^{-n_F/2}$

and where $n = n_M + n_F$;
$f = n - 3$; and
q = the number of linear constraints of the form $\theta_M = \theta_F$, where θ is one of the parameters L_∞, k, t_0.
M and F = males and females, respectively.

This test was developed by Gallant (1975), as described by Cerrato (1990).

The growth curves were fitted under all possible parameter sets, and the best of both the 4- and 5-parameter, models, i.e. those that maximized the log-likelihood, were selected. The resulting 3-, 4- and 5-parameter models were compared with the 6-parameter model by using the above test to determine which of these three models, w, was of minimum complexity and not significantly different from the 6-parameter model Ω. The model selected on the basis of these tests was the simplest model that, in the statistical sense, provided the best description of the data.

Reproductive biology

The gonads of each fish that could be sexed macroscopically were removed and weighed to the nearest 0.01 g. Each gonad was allocated to a maturity stage, based on the scheme of Laevastu (1965), but which, in the case of females, also took into account the histological characteristics of the ovaries (see "Results" section).

The percentage contributions made by the different gonadal stages in sequential 50-mm length intervals were calculated for both female and male *G. hebraicum*. The lengths at which 50% of female and male *G. hebraicum* reach sexual maturity (L_{50}) were determined by fitting the logistic curve to the percentage of female and male fish which, during the spawning period, possessed gonads at stages III to VIII (see "Results" section for rationale for using these six stages for this purpose). The logistic curve was fitted by employing a nonlinear technique (Saila et al., 1988) and by using a routine statistical method provided in SPSS (SPSS Inc., 1988). The logistic equation is $P_L = 1/(1 + e^{(a+bL)})$, where P_L is the proportion of fish with mature gonads at the mid-point of the length class, L, and a and b are constants. The L_{50} for each sex was derived from the equation $L_{50} = \frac{-a}{b}$. The ages at which 50% of females and males reached maturity, i.e. the A_{50}, were estimated, as follows, from the inverse von Bertalanffy growth equations for the two sexes (see Stergiou, 1999):

$$A_{50} = t_0 - \left(\frac{1}{k}\right) \log\left(1 - \frac{L_{50}}{L_\infty}\right).$$

Gonadosomatic indices (GSIs) of females and males $\geq L_{50}$ at first maturity were determined from the equation

$$W1/W2 \times 100,$$

where $W1$ = wet weight of the gonad; and
$W2$ = wet weight of the whole fish.

Mortality

Preliminary analysis of catch curves demonstrated that the mortality estimates derived for commercially and recreationally caught fish that were greater than the MLL of 500 mm and eight years old and thus fully recruited (see "Results" section) were similar. Thus, the data from the commercial and recreational samples were pooled for estimating mortality. An estimate of the instantaneous coefficient of natural mortality, M, was determined from the von Bertalanffy growth coefficient, k, with the regression equation developed by Ralston (1987), i.e. $M = 0.0189 + 2.06k$. The instantaneous coefficient of total mortality, Z, was determined by maximizing the likelihood, when fitting the estimated age composition resulting from that mortality to the observed age composition data for those dhufish that were greater than the MLL of 500 mm and eight years old. In order to assess whether the observed age composition data reflected decreasing levels of total mortality in earlier years, the catch curve analysis was repeated with different initial ages, ranging from 10 to 30 years. Values of Z were also estimated by using the observed maximum age (t_{max}) for the sampled dhufish, employing both the regression equation reported for fish by Hoenig (1983), i.e.

$$\log(Z) = 1.46 - 1.01 \log(t_{max}),$$

and the equation for the expected value of the maximum age in a sample of size n, i.e.

$$E(t_{max}) = \frac{1}{Z} \sum_{i=1}^{n} \frac{1}{i} + t_c,$$

where t_c = the age at which fish become fully recruited to the fishery (Johnson and Kotz, 1970, p. 216, as reported by Hoenig, 1983).

Results

Habitats of *Glaucosoma hebraicum*

Glaucosoma hebraicum <150 mm TL and <14 months old were caught regularly by trawlers offshore in water

depths of 27 to 33 m. The depth sounder indicated that these small *G. hebraicum* were most consistently caught over hard substrate that lay adjacent to reefs—a conclusion later confirmed by video footage. Although a considerable amount of effort and a variety of techniques were employed in attempts to catch fish with lengths of 150–300 mm, only a small number of fish of this size were collected. However, a few *G. hebraicum* of this length class were caught by an experienced spearfisher while diving over low-lying reefs with rock ledges <30 cm high. Large numbers of dhufish >300 mm in length were obtained from rod and handline fishermen who were fishing in waters that were shown by video camera and commercial echo sounders to be located over limestone and coral reef formations and, in particular, where the "drop-offs" (reef edges) were two or more metres in height.

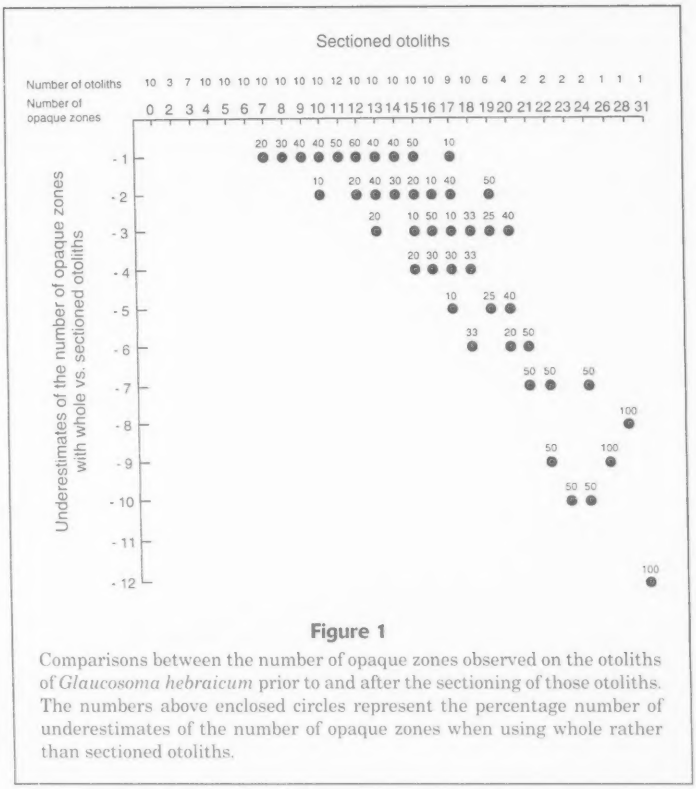
Sectioned otoliths
Number of otoliths
10 3 7 10 10 10 10 10 10 10 12 10 10 10 10 10 9 10 6 4 2 2 2 2 1 1 1
Number of opaque zones
0 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 26 28 31
Underestimates of the number of opaque zones with whole vs. sectioned otoliths
-1
-2
-3
-4
-5
-6
-7
-8
-9
-10
-11
-12

Figure 1

Comparisons between the number of opaque zones observed on the otoliths of *Glaucosoma hebraicum* prior to and after the sectioning of those otoliths. The numbers above enclosed circles represent the percentage number of underestimates of the number of opaque zones when using whole rather than sectioned otoliths.

Comparisons between number of opaque zones visible in whole and sectioned otoliths

The number of opaque zones observed in each sectioned otolith, in which up to six such zones could be seen, was the same as those visible on the same otolith prior to sectioning (Fig. 1). However, this frequently did not apply when a greater number of opaque zones were present. Furthermore, where such discrepancies occurred, the differences between the number of opaque zones detected prior to and after sectioning rose as the number of opaque zones increased. In all cases where there were discrepancies, the number of opaque zones detected after sectioning was greater than prior to sectioning. Underestimates of the number of growth zones with whole otoliths, based on comparisons with those detected in sectioned otoliths, rose from one in whole otoliths with seven to nine opaque zones to between one and seven in those with 10–21 opaque zones (Fig. 1). In otoliths with a large number of opaque zones, the differences sometimes exceeded eight and for one such otolith was as high as twelve. These comparisons demonstrated that, for validation that opaque zones are formed annually and that these zones can thus be used for aging *G. hebraicum*, experiments should be conducted on sectioned otoliths.

Validation that opaque zones are formed annually

The mean monthly marginal increments on sectioned otoliths with 2 to 16 or more opaque zones rose from a low level in January to a maximum in September, before declining precipitously to a minimum in October and then rising slightly in December (Fig. 2). They thus reached high levels in early spring, before declining markedly in mid-spring, as the outermost opaque zone became delineated through the formation of a new translucent zone, and then increased progressively in the ensuing months as the translucent region increased in width. Although fish possessing otoliths with one opaque zone were not caught in all months, the trends exhibited by the mean monthly marginal increments for those months when such fish were caught were consistent with those exhibited by otoliths with a larger number of opaque zones.

Because the mean monthly marginal increment rose and declined only once during the year, irrespective of the number of opaque zones in the otolith, a single opaque zone is laid down in the otoliths of *G. hebraicum* each year. The number of opaque zones in sectioned otoliths can thus be used, in conjunction with the birth date of *G. hebraicum* and the month when the opaque zone(s) become delineated, to age this species.

Growth of *Glaucosoma hebraicum*

Because the trends exhibited by the GSIs and stages in gonadal maturation and oocyte development demonstrated that the spawning of *G. hebraicum* peaked from late January through early February, this species was assigned a birth date of 1 February. Age 0+ *G. hebraicum* were first caught by trawling over hard substrate in April and May, when their lengths ranged from 57 to 81 mm (Fig. 3). However, substantial numbers of the 0+ age class were not

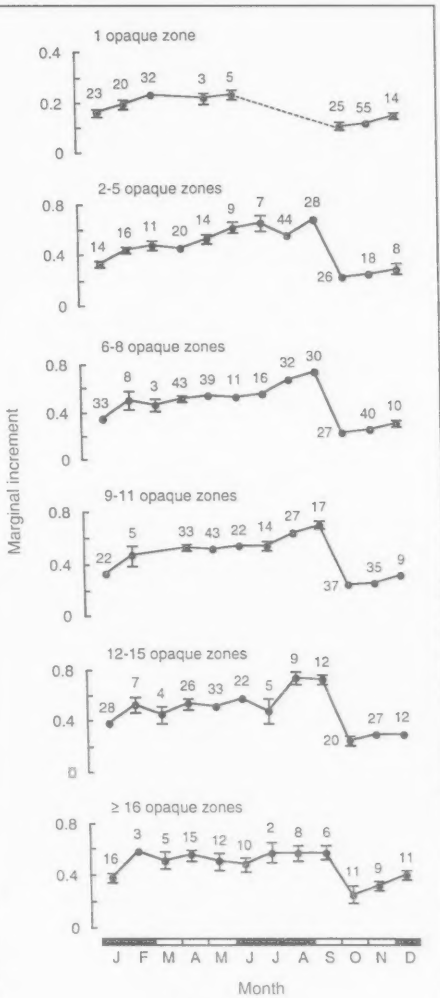

Figure 2

Mean monthly marginal increments ±1SE for sagittal otoliths of *Glaucosoma hebraicum*. Sample size is given for each month. In this Figure and Figure 5, the closed rectangles on the horizontal axis refer to summer and winter months and the open rectangles to autumn and spring months.

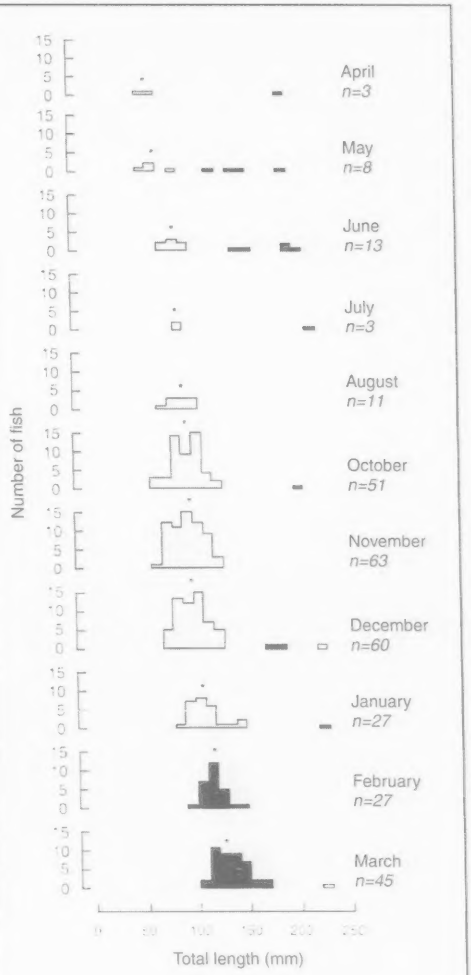

Figure 3

Length-frequency distributions for *Glaucosoma hebraicum* caught by trawling along the lower west coast of Australia by using data for corresponding months in the period May 1996 to June 1999. *denotes mean lengths of 0+ and early 1+ fish. Histograms in gray refer to 0+ fish, and those in black and white refer to 1+ and 2+ fish, respectively.

caught until October, presumably reflecting the time typically required for the 0+ age class to be recruited into these areas from those in which spawning occurs. The mean length of the 0+ age class had reached 95 mm by October, in which month the first opaque zone became delineated on the otoliths, and 108 mm by January, when fish were approaching the end of their first year of life. The mean length of the corresponding cohort, now early 1+, was 127 mm in March, after which month the number of 1+ fish caught in trawl samples declined markedly (Fig. 3).

The best of the 4- and 5-parameter growth curves were selected as the models with the largest log-likelihood at that level of model complexity. The best 4-parameter model was the curve that assumed different asymptotic lengths for the sexes, and the best 5-parameter model was that which assumed that the growth coefficients were equal.

Comparisons between the curves demonstrated that the model that assumed common growth coefficients for females and males was not significantly different ($P>0.05$) from the more complex model, which assumed that all

parameters of the growth curves differed between the sexes. For this curve, the parameters L_∞, k, and t_0 and their 95% confidence limits were estimated to be 929 (908 to 949) mm, 0.111 (0.107 to 0.116)/year, and –0.141 (–0.183 to –0.100) years, respectively, for females, and to be 1025 (1003 to 1048) mm, 0.111 (0.107 to 0.116)/year, and –0.052 (–0.088 to –0.016) years, respectively, for males. The growth curves for females and males were significantly different (P<0.001), with the asymptotic lengths having the most influence on the difference between the sexes. The estimated constant of proportionality between the variance of the residuals and age were 363 for females and 320 for males.

The von Bertalanffy growth curves demonstrated that females grow slightly slower than males. Thus, at ages 2 to 5, females had reached lengths of 196, 273, 342, and 404 mm, compared with 209, 294, 371, and 440 mm for males. By the time *G. hebraicum* had attained 10, 15, and 20 years, the females had reached ca. 628, 756, and 830 mm, respectively, and the males had reached ca. 689, 832, and 914 mm, respectively (Fig. 4). The maximum ages recorded for females and males were 39 and 41 years, respectively, and the maximum total lengths of females and males were 981 mm (=ca. 15.3 kg) and 1120 mm (=ca. 23.2 kg), respectively. The ages at which female and male *G. hebraicum* reach the minimum legal length for capture (500 mm TL) were 7.0 and 6.0 years, respectively.

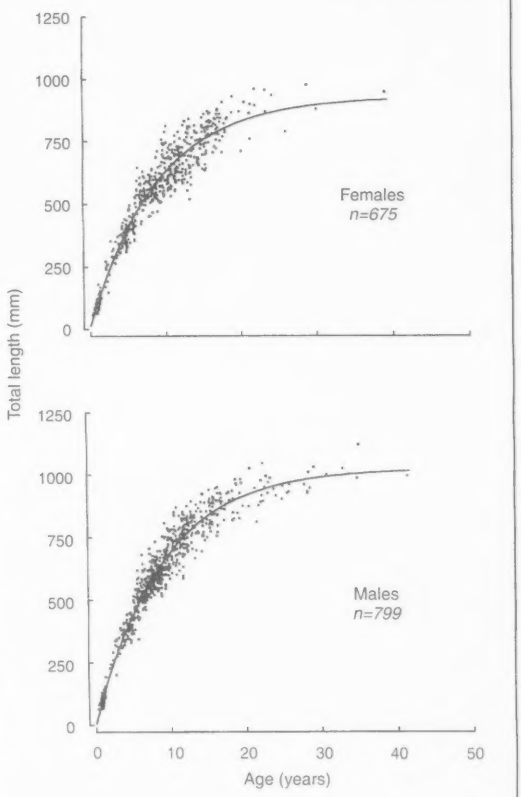

Figure 4

Von Bertalanffy growth curves fitted to length-at-age data for females and males of *Glaucosoma hebraicum* caught on the lower west coast of Australia. n = number of fish used to construct growth curves.

Trends exhibited by reproductive variables

The macroscopic characteristics of the different stages in gonadal development, and of the cytological characteristics of the ovaries at different stages based on an examination of histological sections, are given in Table 1.

Because stages I (virgin) and II (immature) in the development of both the ovaries and testes of *G. hebraicum* were difficult to separate macroscopically, data for these two stages were pooled in the case of both sexes. Furthermore, it is also important to recognize that spawning stage (VI) ovaries are distinguished from prespawning stage (V) ovaries almost exclusively on the basis of their possession of hydrated oocytes or postovulatory follicles (or both) when histological sections were employed to examine the ovary at a finer scale. However, because *G. hebraicum* is a multiple spawner, i.e. produces eggs in batches at intervals, any "prespawning" stage ovary may already have produced some hydrated oocytes, but been at an intermediate phase in which the next batch of yolk granule oocytes had not yet become hydrated. The prevalence of females with prespawning ovaries that had already spawned on one or more occasions would be expected to increase during the spawning period. Likewise, the main difference between prespawning and spawning testes, i.e. the ability of the testes to produce milt when subjected to physical pressure, may often represent different phases in the cyclical changes undergone in the testis during the spawning period. For the above reasons, the data on stage-V and stage-VI ovaries and testes were pooled for describing the change in compositions of the gonadal maturity stages of each sex during the year.

Between May 1996 and April 1998, the mean monthly GSIs for females of *G. hebraicum* that were greater than the L_{50} of 301 mm at first maturity were always low in winter (June to August) and early spring (September), i.e. <1.0 but then rose sharply to reach a peak of ca. 2.8 in mid-summer (January), before declining markedly during early to mid-autumn (March and April) (Fig. 5). The trends displayed by the mean monthly GSIs for males of *G. hebraicum*, that were greater than the L_{50} of 320 mm at first maturity, paralleled those just described for females.

Because the trends exhibited by the mean monthly GSIs for females and males were the same during both 12 month periods, the percentage contributions of the different gonadal stages of the females and males of *G. hebraicum*, that were longer than the L_{50}, were pooled for each of the corresponding calendar months. The gonads of female *G. hebraicum* in July were at stages I–II, i.e. virgin or immature (Fig. 6). Fish with ovaries at stage III (developing) were first found in August, albeit only a few fish, and those at stage IV

Table 1

Characteristics of the macroscopic stages in the development of the gonads of *Glaucosoma hebraicum* and, in the case of the ovaries, the histological characteristics of each corresponding ovarian stage. Terminology for oocyte stages follows Khoo (1979).

Stage	Macroscopic appearance	Histological characteristics
I–II (virgin and immature)	Gonads very small. Ovaries transparent and oocytes not visible. Testes strandlike and gray-white.	Ovigerous lamellae highly organized. Oogonia and chromatin nucleolar oocytes and, in more advanced ovaries, early perinucleolar oocytes are present. These oocyte stages are present in all subsequent ovarian stages.
III (developing)	Gonads slightly larger than at stage I or II. Ovaries pinkish, blood capillaries visible in ovary walls. Testes white and more lobular.	Early and late perinucleolar oocytes and yolk vesicle oocytes present.
IV (maturing)	Gonads markedly larger. Ovaries reddish-orange, capillaries more conspicuous and some yolk granule oocytes visible through ovary wall. Milt is not extruded when pressure is applied to testes.	Yolk vesicle and yolk granule oocytes abundant.
V (prespawning)	Ovaries orange and occupy most of space in body cavity. Extensive capillaries in ovary walls. Milt appears when testes placed under firm pressure.	Yolk granule oocytes abundant and in tight groups.
VI (spawning)	Same as for stage V, but with hydrated oocytes visible through ovarian wall and only slight pressure required to release milt from testes.	Hydrated oocytes or postovulatory follicles (or both) present.
VII (spent)	Gonads smaller than at stages V or VI. Ovaries flaccid. Some yolk granule oocytes still visible through ovary wall. Testes pinkish-red.	Remnant yolk granule oocytes present, typically undergoing atresia.
VIII (recovering spent)	Gonads greatly reduced in size and dark red. Testes strandlike.	Lamellae not organized as in early stages of development and contain extensive scar tissue. Any remaining yolk granule oocytes are atretic.

(maturing) and stages V and VI (prespawning and spawning) were first recorded in September and October, respectively. Stage-V and stage-VI ovaries collectively became the most prevalent group in females in November and formed the most dominant group by far in December to March. The samples in February and March contained a few female fish with stage I–II ovaries, but none with ovaries at either stage III or IV (Fig. 6). These trends provide overwhelming circumstantial evidence that any female whose ovaries have developed to at least stage III by November will progress through to maturity during the following months of the spawning period. Thus, the L_{50} for females at first maturity was calculated by using the percentage of ovaries with stages III and IV, as well as those with stages V–VIII. Although females with stage-VII (spent) and stage-VIII (recovering spent) ovaries were found between January and May, the majority of ovaries were at stages I–II in the latter month and all were at stages I–II in June. The trends exhibited by the pattern of gonadal development in males were essentially the same as those just described for females and thus the L_{50} of males was likewise calculated with the percentage of testes at stages III–VIII (Fig. 7).

The following account of the trends exhibited by the oocyte composition of ovaries is based on an histological examination of the ovaries of large fish well above the L_{50} at first maturity. The oocytes in ovaries in July and August were almost exclusively at the chromatin nucleolar stage. Ovaries with yolk vesicles first appeared in September, and those with yolk granules were first found in October. Yolk granule oocytes became increasingly prevalent in ovaries in November and dominated the complement of their larger oocytes between December and March. Some of the residual yolk granule oocytes in April and all of those in May were undergoing atresia. No yolk vesicle or yolk granule oocytes were found in June. Hydrated oocytes were first found in ovaries in November and were present in many ovaries between December and March and in a few ovaries in April, but were found neither in May nor in the immediately ensuing months. Small numbers of postovulatory follicles were present in about a third of the ovaries of large females caught between December and March. The oocyte diameters of individual large *G. hebraicum* caught in each month of the spawning period produced a series of modes (data not shown).

Length and age at maturity

The sex of *Glaucosoma hebraicum* was not able to be determined by macroscopic examination of the gonads until it had reached ca. 150 mm in length. During the main part of the spawning period, i.e. December to March, the gonads of all female and male *G. hebraicum* <250 mm were at the earliest stages of development, i.e. I–II (Fig. 7). Gonads at stages III–VIII were first found in the 250–299 mm length class of females and in the 300–349 mm length class of males. The presence of such gonads demonstrated that the fish were maturing or that spawning was occurring or had been completed (see earlier). The prevalence of ovaries at stages III–VIII increased to ca. 80% in the 300–349 mm length class and to 100% in all females >450 mm. The gonads of all males >450 mm were at stages III–VIII (Fig. 7). The L_{50}'s for the lengths of female and male *G. hebraicum* at first maturity, derived from the logistic curve fitted to the percentage contributions of fish with gonads at stages III–VIII in sequential 50-mm length classes, were 301 and 320 mm, respectively (Fig. 7).

Individual *G. hebraicum* could first be sexed macroscopically during their second year of life. Although relatively few two-, three- and four-year-old fish were caught, the trends exhibited by the proportion of gonads at stages III–VIII in both sexes during the spawning period were consistent. One female and no males at two years of age possessed gonads at stage III or greater (Fig. 8). However, 50% of three-year-old female and male fish, and all five-year-old females and all six-year-old males possessed such gonads and were thus regarded as mature. The A_{50}'s for the age at first maturity of females and males were 3.4 and 3.3 years, respectively.

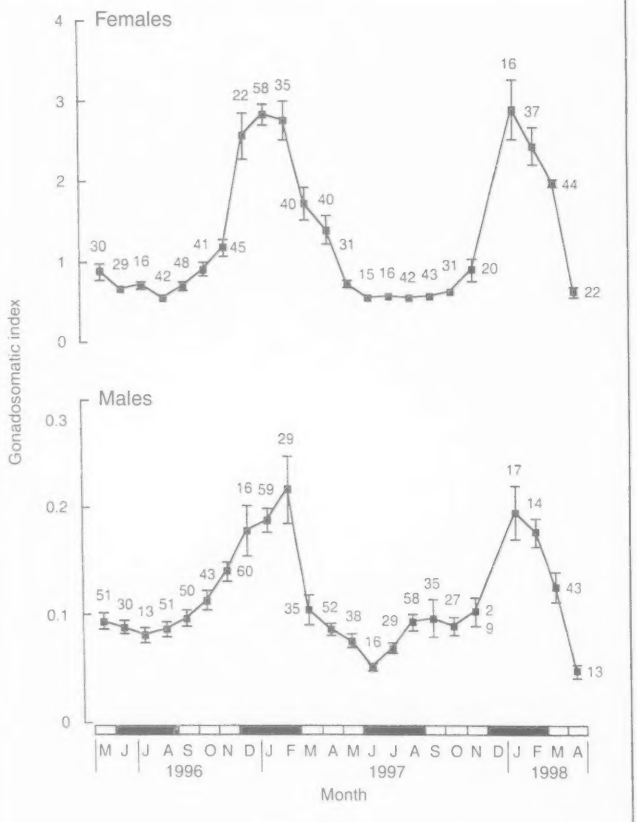

Figure 5

Mean monthly gonadosomatic indices ±1SE for females and males of *Glaucosoma hebraicum* caught in offshore waters between May 1996 and April 1998. Data in this Figure and Figure 6 are restricted to females and males $\geq L_{50}$ at first maturity. Numbers of fish used to calculate each mean GSI are shown.

Mortality

Using the regression equation developed by Ralston (1987), in combination with the estimated value for the von Bertalanffy growth coefficient, k = 0.111/year, we estimated the instantaneous coefficient of natural mortality, M, to be 0.25/year. The catch curve analysis of the combined age composition data, for the 620 dhufish older than 9 years and longer than the MLL (Fig. 9), produced an estimate of the instantaneous coefficient of total mortality, Z, of 0.21/year (95% confidence interval: 0.19 to 0.23/year). The estimate of Z remained at about this level as the initial age was increased to 15 years and then declined to ca. 0.15/year at 24 to 27 years (Fig. 9). It subsequently became less precise as the initial age increased. An estimate of Z of 0.10/year was obtained when the observed maximum age of 41 years was substituted into Hoenig's (1983) regression equation. However, when the sample size of 620 fish was taken into account, with the expression for the expected maximum age (Hoenig 1983, Appendix A), Z was estimated to be 0.22/year.

Discussion

Ontogenetic changes in habitat of *Glaucosoma hebraicum*

Extensive sampling for *G. hebraicum* during the present study, allied with data obtained with an echo sounder and video footage, demonstrate that this species changes habitat as it increases in size. Thus, *G. hebraicum* <150 mm was found to live in areas near reefs where the substrate is firm and sponges often occur (Bergquist and Skinner, 1982). The reduction in the numbers of 1+ dhufish caught by trawling in this type of habitat in late autumn, when their lengths were about 130 mm, probably reflects a movement by the members of this

cohort, as they increase in size, from a habitat that could be trawled to one where reefs occur and where it was not possible to trawl. This conclusion is supported by the fact that the few dhufish of 150–300 mm that were caught were collected from low-lying reefs, i.e. reefs that contained rock ledges up to 30 cm in height. In contrast, *G. hebraicum* >300 mm typically occupy areas where there are substantial limestone and coral reef formations and their large size would make them less susceptible to predation in a habitat where large predatory species, such as the Samson fish (*Seriola hippos*) and the pink snapper (*Pagrus auratus*) are found (Hesp, personal obs.).

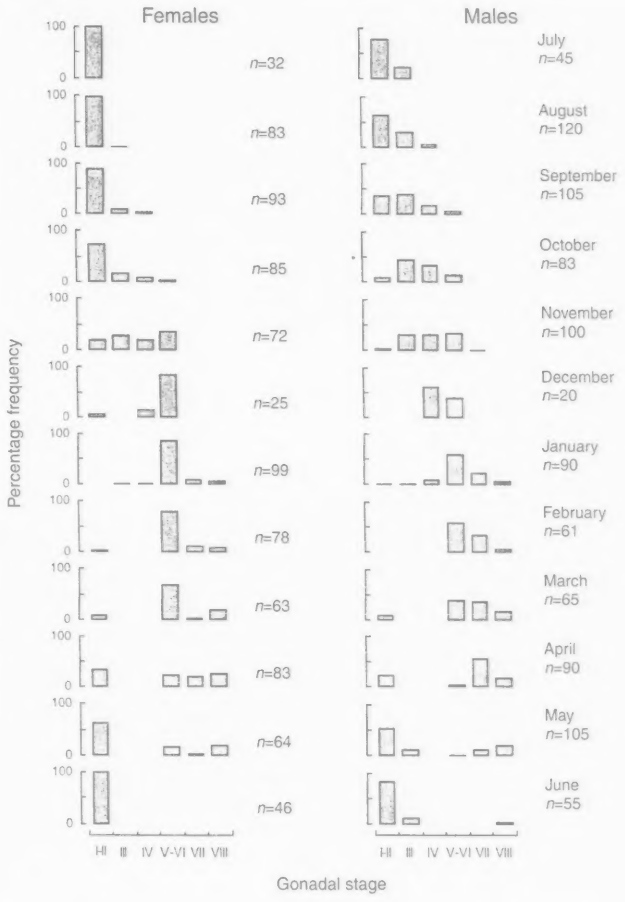

Figure 6

Percentage frequency histograms for gonadal maturity stages of females and males of *Glaucosoma hebraicum*. Data have been pooled for corresponding months in the period May 1996 to April 1998. Sample sizes (n) are given for each month.

Aging

The trends exhibited by the marginal increments on sectioned otoliths of *G. hebraicum* show that an opaque zone is formed annually in the otoliths of this species. However, comparisons between the number of opaque zones on individual otoliths prior to and after sectioning demonstrate that, after this species has reached six years in age, one or more of these zones often become visible only after the otolith has been sectioned. This demonstrates that earlier estimates of the age of older *G. hebraicum*, which were based on the number of opaque zones visible in whole otoliths (Sudemeyer et al.[1]), were almost certainly often too low.

An inability to detect all of the opaque zones in the whole otoliths of older fish is largely attributable to the fact that, as the otolith increases in width, it becomes increasingly difficult to distinguish between the zones at the periphery of the otolith. This problem parallels the situation recorded for several other medium-size to large teleosts, such as Pacific hake (*Merluccius productus*) (Beamish, 1979), starry flounder (*Platyichthys stellatus*) (Campana, 1984) and blue-spotted flathead (*Platycephalus speculator*) (Hyndes et al., 1992). Our results demonstrate that, although most *G. hebraicum* are less than 25 years old, some females and males live for longer than 30 years and very occasionally for up to about 40 years.

Other species that are typically caught by commercial and recreational rod and hand-line fishermen when fishing for dhufish include pink snapper (*Pagrus auratus*), Sampson fish (*Seriola hippos*), silver trevally (*Pseudocaranx dentex*), breaksea cod (*Epinephelides armatus*), and occasionally also King George whiting (*Sillaginodes punctata*). The maximum total lengths and weights recorded for these five species are 1300 mm and 19.5 kg for pink snapper, 1753 mm and 53.6 kg for Samson fish, 938 mm and 10.0 kg for silver trevally, 550 mm and 2.9 kg for breaksea cod, and 690 mm and 4.8 kg for King George whiting, compared with 1219 mm and 25.8 kg for dhufish (Hutchins and Thompson 1995).

Although reliable data have been obtained for the age and growth of a number of commercial and recreational fish species that live in nearshore coastal or estuarine waters in southwestern Australia (e.g. Chubb et al., 1981; Hyndes et al., 1992, 1996; Hyndes and Potter, 1996, 1997; Laurenson et al., 1994; Fairclough et al., 2000; Sarre and Potter, 2000), comparable data for those species that are found in and around reefs in deeper waters in southwestern Australia are restricted to those recorded for *G. hebraicum* in this paper and for the King George whiting *Sillaginodes*

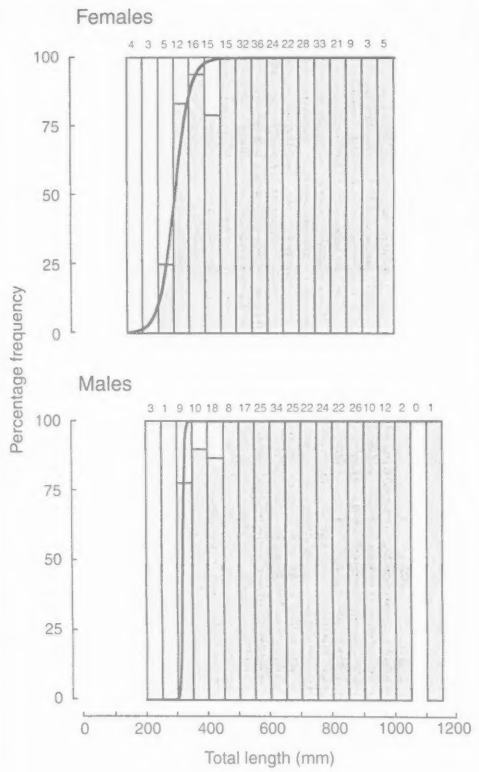

Figure 7

Percentage frequency of occurrence of gonads at stages I–II (□) and stages III–VIII (■) in each sequential 50-mm class of female and male *Glaucosoma hebraicum* caught between December and March. The logistic curve has been fitted to the data for fish with gonads at stages III–VIII. The sample size is given for each length class.

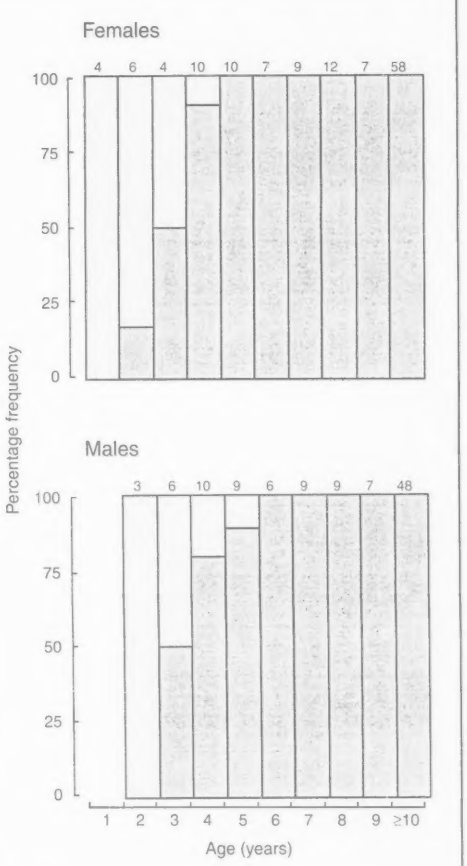

Figure 8

Percentage frequency of occurrence of gonads at stages I–II (□) and stages III–VIII (■) in each sequential age class of female and male *Glaucosoma hebraicum* caught between December and March. The sample size is given for each age class.

punctata by Hyndes et al. (1998). Using data from the lower west coast of Australia, Hyndes et al. (1998) estimated the von Bertalanffy growth parameters, L_∞, k, and t_0, for King George whiting to be 538 mm TL, 0.47/year, and 0.13 years, respectively, for females, and 500 mm TL, 0.53/year and 0.16 years, respectively, for males. Although there are no published studies on the growth of pink snapper and silver trevally in Western Australia, the growth of these two species has been investigated in New Zealand by Francis et al. (1992) and by James (1984) respectively. The parameters L_∞, k, and t_0 were estimated to be 720 mm FL (fork length), 0.106/year and –0.75 years, respectively, for pink snapper, and ranged from 436 to 448 mm FL, from 0.27 to 0.43/year and from –1.6 to –0.6 years, respectively, for silver trevally. Although the growth coefficient, k, for dhufish, i.e. 0.111/year, was similar to that for pink snapper, it was appreciably less that that for both King George whiting and silver trevally. Dhufish had an asymptotic length ca. 35% greater than that of pink snapper and approximately twice those of King George whiting and silver trevally.

The lengths of females at maturity have been reported as ca. 350 mm FL for silver trevally (James, 1984) and 413 mm TL for King George whiting (Hyndes et al., 1998) and have been estimated as 237 mm FL for pink snapper (calculated from Crossland, 1977). Although maturity is first achieved by the females of snapper and dhufish at 30% of their respective asymptotic lengths, it is attained by the females of King George whiting and silver trevally at 75–80% of their asymptotic lengths. This finding implies that the last two species have a higher reproductive load *sensu* Cushing (1981). Thus, although these four species reach maturity and begin to occupy promi-

nent reefs at similar lengths, the growth of silver trevally and King George whiting slows after maturation, whereas that of snapper and dhufish continues appreciably after they have reached maturity.

Spawning location, period, and mode

Glaucosoma hebraicum with gonads at stages VI (spawning) and VII (spent) were caught in waters ranging from 10 to 150 m in depth and at distances of 3 to 50 km from the shore and between latitudes 28°55′ and 32°45′S. Thus, the spawning of dhufish is not apparently restricted to any particular water depth or region along the coast. However, because *G. hebraicum* greater than 300–320 mm in length (their size at first maturity) were almost invariably caught only around limestone or coral reef formations, this species apparently spawns in the vicinity of reefs.

Because hydrated eggs and postovulatory follicles were found in at least some of the ovaries of large females in each month between November and April, it is evident that *G. hebraicum* spawn between the end of spring and middle of autumn. Although some fish commenced spawning in November, the mean GSI of female fish in that month was still well below its maximum. This indication that only a small amount of spawning occurs in November is consistent with the fact that many of the ovaries of large fish were still at stages III and IV. Although most of the ovaries of large females caught in May 1997 contained some vitellogenic oocytes, these oocytes were usually undergoing atresia and the ovaries of other large fish in that month were either spent or resting. Furthermore, none of the ovaries of large *G. hebraicum* caught in May contained hydrated oocytes. This finding provides strong evidence that the spawning period does not extend into May. There is also strong evidence that spawning peaks in January and February. For example, by January, the ovaries and testes of most large fish were at stages V or VI, i.e. prespawning or spawning, and, for the first time, some were spent or even recovering spent (stages VII and VIII). The maintenance of the GSIs of females at their maxima in both January and February is attributable to the fact that, because *G. hebraicum* is a multiple spawner, new batches of hydrated oocytes were continually being developed in the ovary during these two months. However, the GSIs of females and males both declined precipitously in March, which demonstrates that, in the case of ovaries, the release of eggs during spawning was not being compensated for by a comparable production of new batches of mature eggs. As spawning activity peaked in January and February, it was appropriate to use 1 February as the birth date of *G. hebraicum* when assigning an age to each fish.

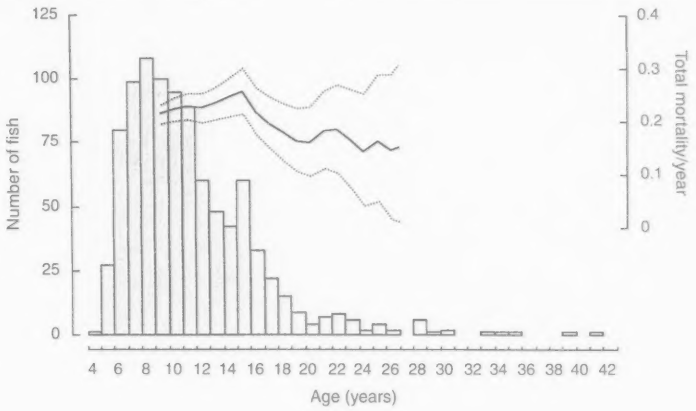

Figure 9

Age composition of *Glaucosoma hebraicum*, that were caught at lengths ≥ the minimum legal length of 500 mm, and maximum likelihood estimates (±95% confidence limits) for the instantaneous coefficients of total mortality/year, *Z*, determined from subsets of these data selected by using different initial ages.

The fact that, during the spawning season, mature ovaries of *G. hebraicum* often contained yolk vesicle, yolk granule, and hydrated oocytes and, in some cases, also postovulatory follicles, implies that this species is a multiple spawner *sensu* deVlaming (1983), i.e. individual females release eggs on more than one occasion in a spawning season. The oocytes of individual female *G. hebraicum* during the spawning period ranged widely in size and, in many cases, their diameters formed relatively discrete modes in oocyte diameter-frequency distributions. The ovaries of *G. hebraicum* thus contain batches of oocytes that are presumably released at different times. Multiple-batch spawning over a protracted period enables a greater total number of eggs to be produced and released during a spawning period and results in eggs becoming discharged at different times (McEvoy and McEvoy, 1992), which would increase the overall chance of recruitment success.

Implications of the biology of *Glaucosoma hebraicum* for fisheries management

The age composition data for dhufish older than 9 years and larger than the MLL reflect an average level of the instantaneous coefficient of total mortality, *Z*, of 0.21/year. This value is consistent with the estimate obtained from the observed maximum age, taking into account the sample size of 620 fish (Hoenig, 1983). The much lower value obtained for *Z*, with Hoenig's (1983) regression equation for fish, i.e. 0.10/year, does not take into account sample size.

The estimate of the instantaneous coefficient of natural mortality, *M*, of 0.25/year, that was calculated with Ralston's (1987) equation, exceeds the average value of 0.21/year for the instantaneous coefficient of total mortality, which was estimated from the catch curve. Examination of the residuals from the regression line fitted by Ralston (Fig. 8.1 in

Ralston, 1987) suggests that the precision of this estimate of the instantaneous coefficient of natural mortality is likely to be relatively low. It was therefore concluded that the value for M derived from Ralston's equation represented an overestimate. A more detailed examination of the catch curve data suggested, but was unable to demonstrate conclusively, that the level of total mortality experienced by the older fish when they were young was less than that which is now being experienced by the population. Indeed, if the decline in the estimated value for Z, displayed in Fig. 9, was extrapolated to an age of 40 years, the total mortality exhibited by the oldest age classes (when, as young fish, they first became fully vulnerable to the fishery) would be ca. 0.1/year. Such a value, which might be only slightly greater than the natural mortality, matches the estimate of Z calculated from the observed maximum age with Hoenig's (1983) regression equation. However, such agreement may be fortuitous because the latter estimate should represent the total mortality experienced by the fish within the sample, i.e. from age 9, rather than just the mortality of the older fish. Nevertheless, if the level of natural mortality, M, is ca. 0.1/year and the average level of instantaneous coefficient of total mortality, Z, from age 9 years is ca. 0.21/year, the current level of fishing mortality, F, would exceed 0.11/year.

In the nearshore waters along the lower west coast of Australia where this species is most heavily fished, the abundance of *G. hebraicum* has declined to a level that is of concern to fishermen. Numerous anecdotal reports indicate that commercial and dedicated recreational fishermen, such as those who provided the samples for this study, now tend to move further offshore in order to obtain catches of *G. hebraicum* comparable with those they used to obtain in waters closer to the coast. However, many recreational fishermen still continue to fish for *G. hebraicum* (and other species) in the traditional areas where dhufish were fished in the past. The expansion of the fishery for dhufish to include waters farther offshore, allied with the increasing use of global positioning systems (GPSs) to improve fishing efficiency, is increasing the level of exploitation of the stock as a whole.

The fact that there are indications that the fishing-induced mortality of dhufish may now exceed natural mortality and that ongoing expansion in the extent to which fishermen are moving offshore (and also, in the case of recreational fishermen, in a northwards and southwards direction from the main metropolitan region of Perth) will further increase fishing pressure, is of concern to the managers responsible for the fishery for *G. hebraicum*. However, because our sampling regime was not designed specifically at determining the levels of fishing mortality to which *G. hebraicum* is being subjected, there is clearly a need to undertake a study in which the main aim is to achieve this objective. If such research were to confirm our preliminary findings that fishing mortality is reaching an unacceptable level, there will be an urgent need to use the biological data produced during the current study to refine the management plans designed to conserve this species.

Female and male *G. hebraicum* first reach sexual maturity at the end of their third year of life when they are just over 300 mm in length and they reach 500 mm, the MLL for capture, when they are about 7 and 6 years old, respectively. Thus, on average, the female and male dhufish that live until they reach the MLL will have had the opportunity to have spawned for four and three years, respectively, before they can legally be retained following capture. Ongoing research at the state fisheries laboratory in Western Australia has indicated that ca. 50% of fish caught in waters of 20–30 m depth die on being released back into the water and that this percentage increases to ca. 95% for fish brought to the surface from depths greater than 40 m (Moran[2]). Thus, the use of a MLL is likely to be of only limited value for conserving this species as fishing effort continues to increase. It is therefore important to introduce measures that will conserve *G. hebraicum* by maintaining the catches of this species at a level consistent with the requirements for ecological sustainability. Examples of such management controls might include closing areas to commercial and recreational fishing (particularly those around reefs that are especially heavily fished) introducing quotas for commercial fish catches, making adjustments to the number of commercial licenses, further restricting the bag limit for recreational fishermen, and limiting the number of recreational fishermen that can fish in a given area. Furthermore, because the Fremantle Maritime Centre has successfully cultured *G. hebraicum* (Cleary et al.[3]), there is also now the potential for restocking this species in areas in which it has become severely depleted.

Acknowledgments

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Longitudinal logbook survey designs for estimating recreational fishery catch, with application to ayu (*Plecoglossus altivelis*)

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Abstract—Longitudinal surveys of anglers or boat owners are widely used in recreational fishery management to estimate total catch over a fishing season. Survey designs with repeated measures of the same random sample over time are effective if the goal is to show statistically significant differences among point estimates for successive time intervals. However, estimators for total catch over the season that are based on longitudinal sampling will be less precise than stratified estimators based on successive independent samples. Conventional stratified variance estimators would be negatively biased if applied to such data because the samples for different time strata are not independent. We formulated new general estimators for catch rate, total catch, and respective variances that sum across time strata but also account for correlation stratum samples. A case study of the Japanese recreational fishery for ayu (*Plecoglossus altivelis*) showed that the conventional stratified variance estimate of total catch was about 10% of the variance estimated by our new method. Combining the catch data for each angler or boat owners throughout the season reduced the variance of the total catch estimate by about 75%. For successive independent surveys based on random independent samples, catch, and variance estimators derived from combined data would be the same as conventional stratified estimators when sample allocation is proportional to strata size. We are the first to report annual catch estimates for ayu in a Japanese river by formulating modified estimators for day-permit anglers.

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Angler surveys are widely used in fishery management to estimate recreational catch, and there is an extensive body of literature on this subject (see Guthrie et al., 1991). Pollock et al. (1994) published a manual on angler survey methods and their applications in fishery management. The first purpose of our study is to make two very important points for the designers of recreational fishery surveys: 1) longitudinal surveys taking repeated measures on the same random sample of anglers or boats over time are better than successive independent surveys if the goal is to determine significant trends in catch and fishing effort, and 2) stratified surveys, or successive independent surveys based on random independent samples of anglers or boats, are better than longitudinal surveys if the goal is to obtain precise estimates of annual total catch and fishing effort. If longitudinal fisheries data sets are used to estimate annual catches, then correlations between monthly sample observations must be taken into account when evaluating the precision of catch estimates. This problem is not addressed in the literature, and the variance estimation procedures for this situation are unclear. The second purpose of our study is to estimate the annual catch of ayu (*Plecoglossus altivelis*) in a river because no estimates have been reported in Japan.

In our study, we formulated a new method for accurate variance estimation with longitudinal fishery data, exemplified by a case study of the recreational fishery for ayu in Nakagawa River in Tochigi Prefecture, Japan (Fig. 1). Annual catch estimates based on sums of monthly estimates were compared with those based on combined data for each angler or boat throughout the fishing season. We demonstrate how use of a design with repeated measures facilitates determination of significant seasonal trends in catches, and show the usefulness of combined (nonstratified) data analysis. We also estimate the total annual catch of the ayu fishery by formulating modified estimators for day-permit anglers (anglers who are granted permits to take fish for one day).

Materials and methods

Case study of ayu

We used longitudinal data collected for the Japanese ayu fishery to compare estimators of effort and catch and their associated variance estimators. Ayu is the most popular target species of recreational anglers in rivers in Japan. In the Nakagawa River (Fig. 1), the upstream run of wild juvenile ayu from the coast begins in late March to early April, and is completed by early July. Ayu mature and spawn from September to November, and then die after spawning. Cooperatives release both hatchery-produced and wild juveniles caught

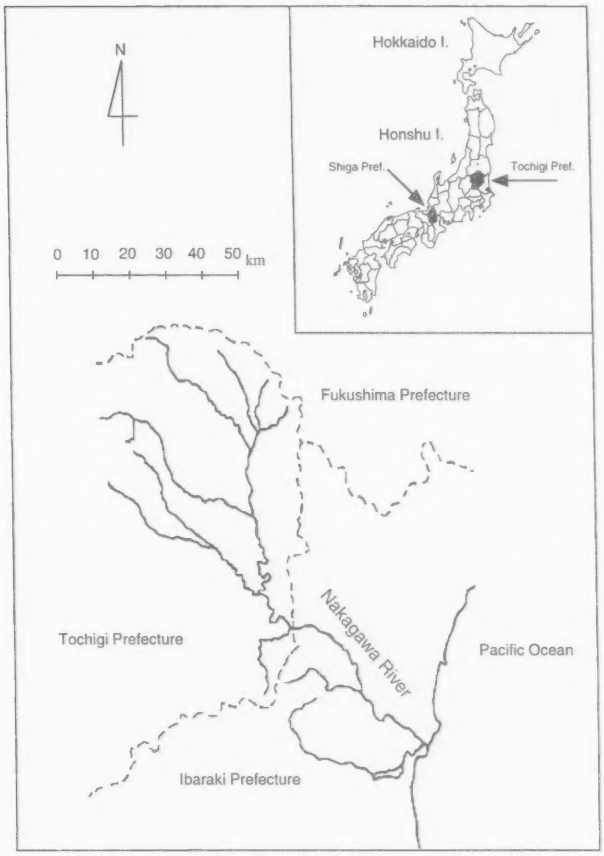

Figure 1

Location of the angler survey. Bold lines in the lower figure indicate the area of the Nakagawa River where the survey was conducted.

in Biwako Lake, Shiga Prefecture (Fig. 1) from early April to the end of May. Thus, recreational anglers catch both naturally recruited wild juveniles and transplanted wild juveniles from Biwako Lake and hatchery-produced ayu released by the cooperatives. Both hatchery and wild stocks consist of a single year class that recruits in the spring. The river fishing season for ayu begins on June 1st and closes at the end of October. To estimate the annual ayu catch by recreational anglers in the Nakagawa River, we conducted a longitudinal log book survey in 1993.

Sampling procedure

There are four cooperatives that set fishing rights on the Nakagawa River in Tochigi Prefecture. Fishing permits for ayu are sold at the cooperatives and fishing tackle shops, and these permits are valid over the entire Nakagawa River in the prefecture. The cooperatives record the total number of season- and day-permits sold, and a complete list of season-permit anglers is available. An *a priori* sample size of 120 anglers (an expected sampling fraction of about 0.5% of the total number of season-permit anglers) was allocated to the four cooperatives in proportion to the number of season-permits sold (Table 1). Anglers who possess a permit (season or day) can fish for ayu over the whole Nakagawa area, regardless of where the permit was purchased. Hence, we treated the samples as if they were drawn from the population by simple random sampling, even though they were drawn by stratified random sampling of cooperatives.

We asked the cooperatives to select samples randomly, but the samples were drawn arbitrarily. The selection, however, was not a purposive sampling; therefore we treated them as random samples. The sampled season-permit anglers were asked to record catch data throughout the fishing season, including each fishing date, the number of ayu caught, and the fishing site, on a printed form, which was returned after the fishing season was over. To estimate the total catch in weight, we also surveyed the body weights of ayu in recreational catches by month. The

Table 1

The number of permits sold in 1993, sample size, and the number of logbooks returned by the four fishermen's cooperative associations along the Nakagawa River. n = number of anglers sampled.

Fishermen's cooperative associations	Number of season permits sold	Number of day permits	n	Number of logbooks returned
Hokubu	11,314	6520	70	64
Nanbu	6391	1946	30	21
Chuo	1911	231	10	10
Motegi	2346	369	10	9
Total	21,962	9066	120	104

primary sampling unit in a population of season-permit anglers or boat owners (i.e. party-boat owners or personal-boat owners) was an angler or a boat owner, and the secondary sampling unit was a fishing day. We selected anglers or boat owners by simple random sampling without replacement from a list of anglers or boat owners, and asked a sample of anglers or boat owners to record catch data on all fishing days throughout the survey. Because all the secondary sampling units were surveyed, we regarded this as a single-stage cluster sampling procedure (Cochran, 1977).

Estimation of total catch by month

Estimation for season-permit anglers or boat owners The principal notations for estimation of the total catch for season-permit anglers or party-boat owners are as follows (Cochran, 1977; Pollock et al., 1994):

N = total number of sampling units (season-permit angler or party-boat or personal-boat owner; known number);
n = sample size drawn from the population N;
M_k = total number of fishing days in the population in kth month (to be estimated);
M_{ik} = total number of fishing days in kth month of selected ith sample;
$\overline{M}_k$ = mean number of fishing days per sampling unit in kth month (to be estimated);
C_{ik} = number of fish caught by ith sample in kth month;
R_k = catch rate of kth month (to be estimated);
C_k^{ss} = total catch by season-permit anglers or by party-boat owners or personal-boat owners in kth month (to be estimated).

The catch rate is the number of fish caught per sampling unit each day. For logbook surveys, the ratio of the mean is the preferable estimator of catch rate (Jones et al.,1995; Pollock et al., 1997).

The ratio and the variance for the catch rate is estimated by

$$\hat{R}_k = \frac{\sum_{i=1}^{n} C_{ik}}{\sum_{i=1}^{n} M_{ik}}, \tag{1}$$

$$\hat{V}(\hat{R}_k) \simeq \frac{N}{M_k^2}\frac{N-n}{n(n-1)}\sum_{i=1}^{n}(C_{ik}-M_{ik}\hat{R}_k)^2. \tag{2}$$

This variance estimator is obtained by dividing Equation 6.9 in Cochran (1977, p. 155) by the total number of fishing days in the kth month M_k. In Equation 2, M_k is unknown; hence we approximated the variance estimate by using the estimator of M_k as follows (Thompson, 1992, p. 62):

$$\hat{V}(\hat{R}_k) = \frac{N-n}{N\hat{\overline{M}}_k^2 n(n-1)}\sum_{i=1}^{n}(C_{ik}-M_{ik}\hat{R}_k)^2, \tag{3}$$

where $\hat{M}_k = N\hat{\overline{M}}_k$. The variance of $\hat{M}_k$ is estimated by $\hat{V}(\hat{M}_k) = N^2\hat{V}(\hat{\overline{M}}_k)$, where $\overline{M}_k$ is the mean number of fishing days per sampling unit in kth month. The estimator and the variance are as follows (Cochran, 1977, p. 249, from Eq. 9A.2):

$$\hat{\overline{M}}_k = \frac{1}{n}\sum_{i=1}^{n} M_{ik}, \tag{4}$$

$$\hat{V}(\hat{\overline{M}}_k) = \frac{N-n}{Nn(n-1)}\sum_{i=1}^{n}(M_{ik}-\hat{\overline{M}}_k)^2. \tag{5}$$

The total number of fish caught in kth month is estimated by

$$\hat{C}_k^{ss} = \hat{M}_k\hat{R}_k = N\hat{\overline{M}}_k\hat{R}_k = N\frac{\sum_{i=1}^{n} M_{ik}}{n}\frac{\sum_{i=1}^{n} C_{ik}}{\sum_{i=1}^{n} M_{ik}} = \frac{N}{n}\sum_{i=1}^{n} C_{ik}. \tag{6}$$

This results in an unbiased estimator. When the total number of fishing days M_k is unknown, the ratio estimator coincides with the unbiased estimator. The variance is evaluated by (Cochran, 1977, p. 249, from Eq. 9A.2):

$$\hat{V}(\hat{C}_k^{(st)}) = \frac{N(N-n)}{n(n-1)} \sum_{i=1}^{n} (C_{ik} - \hat{\bar{C}}_k)^2 \quad (7)$$

where $\hat{\bar{C}}_k = \sum_{i=1}^{n} C_{ik} / n$.

Estimation for day-permit anglers We estimated the catch of day-permit anglers separately. The notations for day-permit anglers catch estimation are as follows:

D = total number of day-permits sold through the season (known);
D_k = total number of day-permits sold in k th month (known);
d_k = total number of day-permit anglers who returned logbooks in kth month;
$R_k^{(d)}$ = catch rate of kth month for day-permit anglers;
$C_k^{(d)}$ = total catch by day-permit anglers in kth month (to be estimated).

The estimator of total number of fish caught by day-permit anglers in kth month is

$$\hat{C}_k^{(d)} = D_k \hat{R}_k^{(d)}, \quad (8)$$

where the catch rate for day-permit anglers, estimated by the sample mean, is

$$\hat{R}_k^{(d)} = \frac{1}{d_k} \sum_{i=1}^{d_k} c_{ik}. \quad (9)$$

The variance estimator of $\hat{C}_k^{(d)}$ is (Cochran, 1977, p. 26, from Eq. 2.20):

$$\hat{V}(\hat{C}_k^{(d)}) = D_k^2 \hat{V}(\hat{R}_k^{(d)}) = \frac{D_k(D_k - d_k)}{d_k(d_k - 1)} \sum_{i=1}^{d_k} (C_{ik} - \hat{R}_k^{(d)})^2. \quad (10)$$

Total monthly catch of season- and day-permit anglers The total catch by season- and day-permit anglers in kth month is C_k, which is estimated by

$$\hat{C}_k = \hat{C}_k^{(s)} + \hat{C}_k^{(d)}. \quad (11)$$

These two total estimates are obtained from independent samples (season- and day-permit anglers); therefore the variance is estimated by adding the variances:

$$\hat{V}(\hat{C}_k) = \hat{V}(\hat{C}_k^{(s)}) + \hat{V}(\hat{C}_k^{(d)}). \quad (12)$$

The total catches in weight in kth month are estimated by using the mean body weight of the species in kth month ($\bar{w}_k$) estimated from the survey of individual body weights by

$$\hat{W}_k = \hat{W}_k^{(s)} + \hat{W}_k^{(d)} = \hat{C}_k \hat{\bar{w}}_k, \quad (13)$$

where $\hat{W}_k^{(s)}$ and $\hat{W}_k^{(d)}$ are the total catches in weight for season- and day-permit anglers, given by $\hat{W}_k^{(s)} = \hat{C}_k^{(s)} \hat{\bar{w}}_k$ and $\hat{W}_k^{(d)} = \hat{C}_k^{(d)} \hat{\bar{w}}_k$. In general, season-permit and day-permit anglers fish in the same location; therefore we assumed the same mean body weight for both kinds of anglers. The samples for estimating C_k and $\bar{w}_k$ are independent; therefore the variances are estimated by using Goodman's (1960) formula:

$$\hat{V}(\hat{W}_k) = \hat{V}(\hat{W}_k^{(s)}) + \hat{V}(\hat{W}_k^{(d)}) \quad (14)$$

where $\hat{V}(\hat{W}_k^{(s)}) = \hat{\bar{w}}_k^2 \hat{V}(\hat{C}_k^{(s)}) + \hat{C}_k^{(s)2} \hat{V}(\hat{\bar{w}}_k) + \hat{V}(\hat{C}_k^{(s)}) \hat{V}(\hat{\bar{w}}_k)$

and $\hat{V}(\hat{W}_k^{(d)}) = \hat{\bar{w}}_k^2 \hat{V}(\hat{C}_k^{(d)}) + \hat{C}_k^{(d)2} \hat{V}(\hat{\bar{w}}_k) + \hat{V}(\hat{C}_k^{(d)}) \hat{V}(\hat{\bar{w}}_k)$.

The mean body weight of fish in kth month is estimated from a survey of individual body weights (w_{ik} of l_k fish caught on the fishing grounds). The estimator for kth month and its variance estimator are

$$\hat{\bar{w}}_k = \sum_{i=1}^{l_k} w_{ik} / l_k$$

and $$\hat{V}(\hat{\bar{w}}_k) = \sum_{i=1}^{l_k} (w_{ik} - \hat{\bar{w}}_k)^2 / (l_k(l_k - 1)).$$

The total fishing days in kth month is estimated as the sum of the fishing days estimates of the season-permit anglers and the day-permit anglers by

$$\hat{M}_{Tk} = \hat{M}_k + D_k \quad (15)$$

and the variance is estimated by $\hat{V}(\hat{M}_{Tk}) = N^2 \hat{V}(\hat{\bar{M}}_k)$ because D_k is known.

Estimation of annual catch

Method 1 (based on monthly estimates) The annual catch is estimated by summing monthly catch estimates over the entire fishing season (K months). The point estimator is

$$\hat{C} = \sum_{k=1}^{K} \hat{C}_k = \sum_{k=1}^{K} \hat{C}_k^{(s)} + \sum_{k=1}^{K} \hat{C}_k^{(d)} = \hat{C}^{(s)} + \hat{C}^{(d)}. \quad (16)$$

When the same sample of anglers reports catches throughout the season, the sampling is not independent in each month, and monthly catch estimates are auto-correlated. Taking this correlation into account, the variance estimator is

$$\begin{aligned} \hat{V}(\hat{C}) &= \hat{V}(\hat{C}^{(s)}) + \hat{V}(\hat{C}^{(d)}) \\ &= \sum_{k=1}^{K} \hat{V}(\hat{C}_k^{(s)}) + 2 \sum_{k \le k'}^{K} \widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)}) \\ &\quad + \sum_{k=1}^{K} \hat{V}(\hat{C}_k^{(d)}) + 2 \sum_{k \le k'}^{K} \widehat{\mathrm{Cov}}(\hat{C}_k^{(d)}, \hat{C}_{k'}^{(d)}). \end{aligned} \quad (17)$$

The covariance between two total estimates of season-permit anglers is estimated by (see Appendix 1, from Cochran, 1977, p. 25)

$$\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)}) = \frac{N(N-n)}{n(n-1)} \sum_{i=1}^{n} (C_{ik} - \hat{\bar{C}}_k)(C_{ik'} - \hat{\bar{C}}_{k'}). \quad (18)$$

The fourth term of Equation 17 is equal to 0 if a different sample of day-permit anglers is drawn in each month.

The total catch in weight is estimated by

$$\hat{W} = \sum_{k=1}^{K} \hat{W}_k = \sum_{k=1}^{K} \hat{W}_k^{(s)} + \sum_{k=1}^{K} \hat{W}_k^{(d)} = \hat{W}^{(s)} + \hat{W}^{(d)} \quad (19)$$

and the variance estimator is similar to Equation 17 but has a slightly different covariance which is

$$\widehat{\mathrm{Cov}}(\hat{W}_k^{(s)}, \hat{W}_{k'}^{(s)}) \sim \hat{\bar{w}}_k \hat{\bar{w}}_{k'} \widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)}). \quad (20)$$

This covariance estimator was derived by the delta method (Seber, 1982, p. 7, see Appendix 2), which coincides with a covariance when $\hat{\bar{w}}_k$ and $\hat{\bar{w}}_{k'}$ are constant.

The mean annual catch rate is estimated for season-permit anglers or boats by

$$\hat{R}^{(s)} = \frac{\hat{C}^{(s)}}{\hat{M}^{(s)}}, \quad (21)$$

where $\hat{M}^{(s)} = \sum_{k=1}^{K} \hat{M}_k = N \sum_{k=1}^{K} \hat{\bar{M}}_k$.

Here $\hat{\bar{M}}_k$ is given by Equation 4. The total effort is estimated by $\hat{M}^{(s)} + D$. The approximate variance of $\hat{V}(\hat{R}^{(s)})$ is given by the delta method (Seber, 1982, p. 7; Appendix 3), that is

$$\hat{V}(\hat{R}^{(s)}) \simeq \frac{1}{\hat{M}^{(s)2}} \left\{ \begin{array}{l} \hat{V}(\hat{C}^{(s)}) + \left(\dfrac{\hat{C}^{(s)}}{\hat{M}^{(s)}} \right)^2 \hat{V}(\hat{M}^{(s)}) \\ -2 \dfrac{\hat{C}^{(s)}}{\hat{M}^{(s)}} (\widehat{\mathrm{Cov}}(\hat{C}^{(s)}, \hat{M}^{(s)}) \end{array} \right\}, \quad (22)$$

where $\hat{V}(\hat{C}^{(s)})$ is given by Equation 17, and the variance of the total number of fishing days is estimated by

$$\hat{V}(\hat{M}^{(s)}) = N^2 \left\{ \sum_{k=1}^{K} \hat{V}(\hat{\bar{M}}_k) + 2 \sum_{k \le k'}^{K} \widehat{\mathrm{Cov}}(\hat{\bar{M}}_k, \hat{\bar{M}}_{k'}) \right\}. \quad (23)$$

Here $\hat{V}(\hat{\bar{M}}_k)$ is given by Equation 5 and the covariance of two sample means is estimated by (Cochran, 1977, p. 25)

$$\widehat{\mathrm{Cov}}(\hat{\bar{M}}_k, \hat{\bar{M}}_{k'}) = \frac{N-n}{Nn(n-1)} \sum_{i=1}^{n} (M_{ik} - \hat{\bar{M}}_k)(M_{ik'} - \hat{\bar{M}}_{k'}). \quad (24)$$

The estimator of covariance between $\hat{C}^{(s)}$ and $\hat{M}^{(s)}$ is similar to Equation 18 (see Appendix 1):

$$\widehat{\mathrm{Cov}}(\hat{C}^{(s)}, \hat{M}^{(s)}) = \frac{N(N-n)}{n(n-1)} \sum_{i=1}^{n} (C_i - \hat{\bar{C}})(M_i - \hat{\bar{M}}), \quad (25)$$

where C_i and M_i are the number of fish caught and the number of fishing days of ith season-permit angler or boat owner throughout the season, respectively, and

$$\hat{\bar{C}}_k = \sum\nolimits_{i=1}^{n} C_{ik} / n.$$

and

$$\hat{\bar{M}} = \sum\nolimits_{i=1}^{n} M_i / n.$$

The mean number of fishing days per sampling unit (season-permit angler or boat) is estimated by

$$\hat{\bar{M}} = \frac{\hat{M}^{(s)}}{N}$$

and the variance estimator is

$$\hat{V}(\hat{\bar{M}}) = \frac{1}{N^2} \hat{V}(\hat{M}^{(s)}),$$

where $\hat{M}^{(s)}$ and $\hat{V}(\hat{M}^{(s)})$ are already derived from Equation 21 and Equation 23, respectively.

The catch rate of day-permit anglers over the season is estimated by

$$\hat{R}^{(d)} = \frac{\hat{C}^{(d)}}{D}$$

and the variance is

$$\hat{V}(\hat{R}^{(d)}) = \frac{1}{D^2} \hat{V}(\hat{C}^{(d)}),$$

where $\hat{C}^{(d)}$ and $\hat{V}(\hat{C}^{(d)})$ are given in Equation 8 and Equation 10, respectively.

Method 2 (based on total annual catch of each angler or boat owner) Another procedure for estimating annual catch is to use annual data rather than monthly catch for individual anglers or boats. The advantages of this procedure are that covariances between months do not have to be considered and estimators are much less complicated than those obtained using method 1. Equations derived for monthly estimation can be used without modification for this procedure.

Modified estimators for day-permit anglers

We could not conduct a survey of day-permit anglers, so we substituted $\hat{R}_k$ for $\hat{R}_k^{(d)}$ in Equation 8. In addition, the total number of day permits sold in kth month (D_k) was

unknown. Hence, we slightly modified the procedure for estimating D_k by $D\hat{p}_k$, where p_k is the proportion of day permits sold in kth month to the annual total number of day permits sold (D).

Day permits issued by the cooperatives are sold mainly in fishing tackle shops. We selected four tackle shops and surveyed the total number of day permits sold at the selected jth fishing tackle shop (D_j), and the total number of day permits sold at the selected jth fishing tackle shop in kth month (D_{jk}). The proportion of day permits sold in kth month was estimated by

$$\hat{p}_k = \frac{\sum_{j=1}^{h} D_{jk}}{\sum_{j=1}^{h} D_j},$$

where h is the number of fishing tackle shops selected from a total of H shops. The evaluation of the variance of $\hat{p}_k$ was similar to Equation 3:

$$\hat{V}(\hat{p}_k) = \frac{H(H-h)}{D^2 h(h-1)} \sum_{j=1}^{h} (D_{jk} - D_j \hat{p}_k)^2.$$

Some day permits, however, were sold at the fishing sites, and the above variance estimator was not appropriate for this situation. Assuming $\Sigma_{j=1}^{h} D_j$ was selected by simple random sampling from D, we evaluated the variance by (Cochran, 1977, p. 52, Eq. 3.8)

$$\hat{V}(\hat{p}_k) = \frac{D - \sum_{j=1}^{h} D_j}{D\left(\sum_{j=1}^{h} D_j - 1\right)} \hat{p}_k(1-\hat{p}_k).$$

The modified estimator for the total number of fish caught by day-permit anglers in kth month is

$$\hat{C}_k^{(d)} = D\hat{p}_k\hat{R}_k. \tag{26}$$

Here $\hat{p}_k$ and $\hat{R}_k$ are independent because these are estimated from different survey data. The variance of revised $\hat{C}_k^{(d)}$ was estimated by using Goodman's (1960) method:

$$\hat{V}(\hat{C}_k^{(d)}) = D^2\left\{\hat{R}_k^2\hat{V}(\hat{p}_k) + \hat{p}_k^2\hat{V}(\hat{R}_k) + \hat{V}(\hat{p}_k)\hat{V}(\hat{R}_k)\right\}.$$

The total fishing days in kth month was estimated by Equation 15 but in this case D_k was unknown. The modified estimator was

$$\hat{M}_{Tk} = \hat{M}_k + D\hat{p}_k$$

and the variance was slightly revised as

$$\hat{V}(\hat{M}_{Tk}) = N^2\hat{V}(\bar{\hat{M}}_k) + D^2\hat{V}(\hat{p}_k).$$

The annual catch was estimated by Equation 16, substituting Equation 8 by Equation 26. In this case, we estimated $\hat{C}_k^{(d)}$ and $\hat{C}_{k'}^{(d)}$ from the same sample of season-permit anglers. Hence, the fourth term of the covariance in Equation 17 must be considered. The approximate covariance is estimated by (see Appendix 4)

$$\widehat{\mathrm{Cov}}(\hat{C}_k^{(d)}, \hat{C}_{k'}^{(d)}) = D^2\hat{p}_k\hat{p}_{k'}\widehat{\mathrm{Cov}}(\hat{R}_k, \hat{R}_{k'}), \tag{27}$$

where the covariance between $\hat{R}_k$ and $\hat{R}_{k'}$ is

$$\widehat{\mathrm{Cov}}(\hat{R}_k, \hat{R}_{k'}) \simeq \frac{1}{N^4}\begin{pmatrix} \dfrac{1}{\hat{\bar{M}}_k\hat{\bar{M}}_{k'}}\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)}) \\ -\dfrac{\hat{C}_{k'}^{(s)}}{\hat{\bar{M}}_k\hat{\bar{M}}_{k'}^2}\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{\bar{M}}_{k'}) \\ -\dfrac{\hat{C}_k^{(s)}}{\hat{\bar{M}}_k^2\hat{\bar{M}}_{k'}}\widehat{\mathrm{Cov}}(\hat{\bar{M}}_k, \hat{C}_{k'}^{(s)}) \\ +\dfrac{\hat{C}_k^{(s)}\hat{C}_{k'}^{(s)}}{\hat{\bar{M}}_k^2\hat{\bar{M}}_{k'}^2}\widehat{\mathrm{Cov}}(\hat{\bar{M}}_k, \hat{\bar{M}}_{k'}) \end{pmatrix}.$$

Here $\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)})$ and $\widehat{\mathrm{Cov}}(\hat{\bar{M}}_k, \hat{\bar{M}}_{k'})$ are already given by Equation 18 and Equation 24. The other covariance components are

$$\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{\bar{M}}_{k'}) = \frac{N-n}{n^2(n-1)}\sum_{i=1}^{n}(C_{ik} - \hat{\bar{C}}_k)(M_{ik'} - \hat{\bar{M}}_{k'})$$

$$\widehat{\mathrm{Cov}}(\hat{\bar{M}}_k, \hat{C}_{k'}^{(s)}) = \frac{N-n}{n^2(n-1)}\sum_{i=1}^{n}(C_{ik'} - \hat{\bar{C}}_{k'})(M_{ik} - \hat{\bar{M}}_k).$$

The annual catch in weight was estimated by Equation 19, substituting Equation 8 with Equation 26. The covariance in the fourth term of $\hat{V}(\hat{W})$ in Equation 17 was estimated with Equation 20 by

$$\widehat{\mathrm{Cov}}(\hat{W}_k^{(d)}, \hat{W}_{k'}^{(d)}) = \hat{\bar{w}}_k\hat{\bar{w}}_{k'}\widehat{\mathrm{Cov}}(\hat{C}_k^{(d)}, \hat{C}_{k'}^{(d)})$$

where $\widehat{\mathrm{Cov}}(\hat{C}_k^{(d)}, \hat{C}_{k'}^{(d)})$ is given in Equation 27.

Results

In 1993, 21,962 season permits and 9066 day permits were sold (Table 1). The total number of day permits sold at the four fishing tackle shops was 4776, and the number (proportion, $\hat{p}_k$) sold was 2732 (0.572) in June, 1,189 (0.249) in July, 716 (0.150) in August, 124 (0.026) in September, and 15 (0.003) in October.

We received 104 logbooks from the 120 season-permit anglers sampled, a return rate of 86.7%. In addition, two anglers voluntarily submitted logbooks, but we did not include these unsolicited returns because they were not randomly selected. The modes of the catch rates by the sampled anglers were from five to ten fish per month (Fig. 2). The histograms show a large variation in the catch rate among season-permit anglers. The peak fishing season was from June to July. In September, the number of anglers decreased, and the fishing season ended in October. The

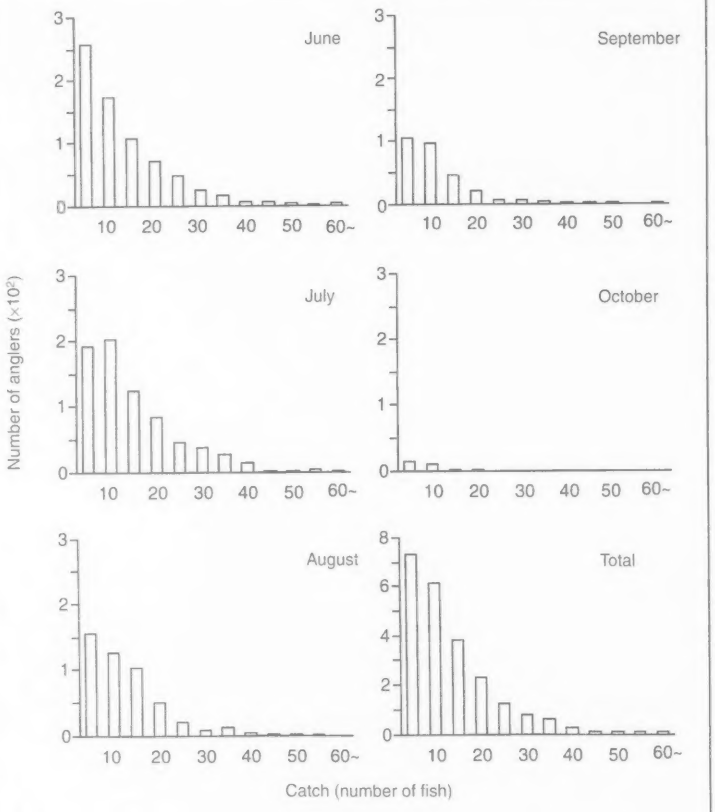

Figure 2

Distributions of the catch rate of ayu by month for 104 sampled season-permit anglers in the Nakagawa River.

modes of the number of fishing days per season-permit angler were five for all months. The variation in the number of fishing days among anglers was also large (Fig. 3).

Monthly plots of the total number of fish caught versus the number of fishing days showed linear relationships (Fig. 4). The variation in Figure 4 indicates differences in the skill of the anglers. The monthly number of anglers decreased over the fishing season. Figure 5 shows the monthly changes in the total number of fishing days, the total number of fish caught, and the catch rate for the 104 sampled anglers. The decline in number of fish caught was largely due to the decrease in fishing days. The change in catch rate indicated a decline in the abundance of the stock.

The mean body weight of ayu was greatest in June (Fig. 6) and was affected by a method of fishing for ayu called "Tomo-zuri" angling, which takes advantage of the attacking behavior of ayu when another fish enters its territory. Anglers attach a "call" fish (a live ayu) above a treble hook that snares the territorial wild fish, as it attacks the "call" fish. Because larger individuals establish territories earlier than smaller ayu, fish caught in June were predominantly the larger individuals.

Reflecting the monthly trend in the number of fishing days, 89% of the total annual catches of season-permit anglers and 98% of those of day-permit anglers were taken from June to August (Table 2). The catch by day-permit anglers was substantially smaller than anticipated, estimated at about 2% of season-permit anglers' catch in both numbers and total weight. CVs ranged from 7% to 12% in June and July for all parameters; however, they were higher in August and September, ranging from 10% to 20%. In October, CVs exceeded 43% for total catch in number and weight. The decreasing precision of the monthly catch rate estimates was caused by the decrease in anglers (n_k) (Figs. 4 and 5).

The CVs of annual estimates of $\overline{M}$ and $\hat{M}_T$ by method 1 were about 7%, but that of $\hat{R}^{(s)}$ was about 20% (Table 2) because we evaluated the covariance terms for the number of catches and fishing days between months; those were

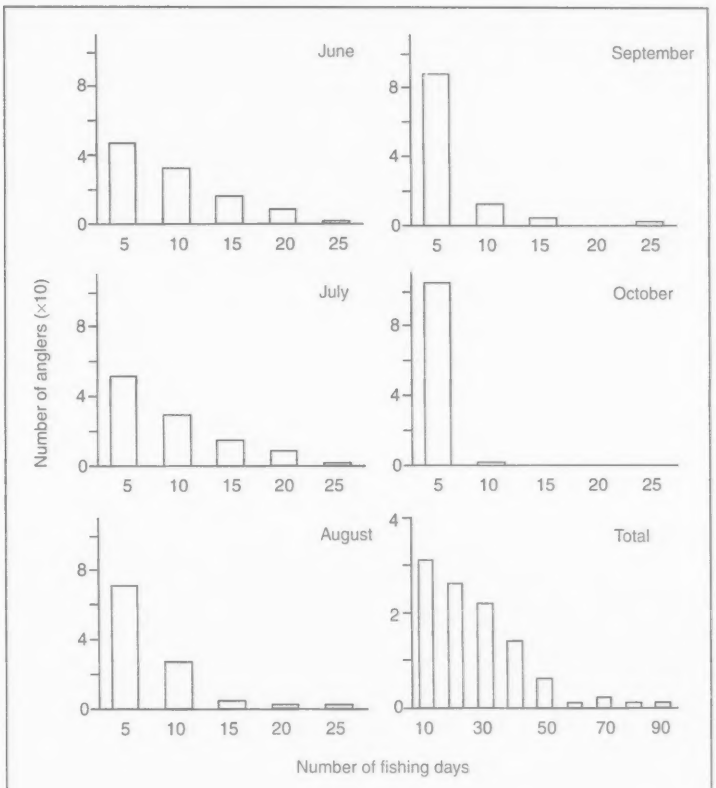

Figure 3

Distributions of the ayu fishing days per angler by month for 104 sampled season-permit anglers in the Nakagawa River.

$\widehat{\mathrm{Cov}}(\hat{C}_k^{(st)}, \hat{C}_{k'}^{(st)})$ in $\hat{V}(\hat{C}^{(st)})$ and $\widehat{\mathrm{Cov}}(\hat{\overline{M}}_k, \hat{\overline{M}}_{k'})$ in Equation 22. The CVs of $\hat{C}$ and $\hat{W}$ were also evaluated at about 21% and were strongly affected by the covariances between months in Equation 17. The variance of the total number estimate $\hat{V}(\hat{C})$ was 1.2604×10^{12}, and variance by neglecting the covariance term in Equation 17 was 1.2230×10^{11}. The CV of $\hat{C}$ without the covariance term was 6.53%. If we neglect the covariance, the variance is substantially underestimated. The variance was 10.31 times larger when the covariance term was included.

We obtained similar point estimates of annual catch by method 2 ($\mathrm{Total}^{\mathrm{meth.2}}$ in Table 2). The CVs of $\hat{\overline{M}}, \hat{\overline{M}}_T, \hat{C}$, and $\hat{W}$ for day-permit anglers were about 7%, but that of $\hat{R}^{(st)}$ was reduced from 19.7% to 6.6% by not considering the covariance terms. The CVs of $\hat{C}$ and $\hat{W}$ dropped about 10% from 21% without the covariance. Similar point estimates and smaller variance estimates were obtained. The variance estimate of the annual catch obtained by method 1 with covariances (1.2604×10^{12}) was 4.11 times larger than that by method 2 (3.0667×10^{11}).

The relationship between the sample size and the precision of the annual catch estimate for season-permit anglers was examined. We calculated the values $\hat{V}(\hat{C})$ for various values of n by using Equation 7. To obtain precision over the season for CVs of $\hat{C}^{(st)}(=\sqrt{\hat{V}(\hat{C})}/\hat{C})$ below 10%, a sample size of 120 or more is required (Table 3).

A high positive correlation in catches between adjacent months was detected (Table 4). We mapped anglers (objects) and fishing days (categories) into a two-dimensional graph by correspondence analysis (Hayashi, 1950; Benzécri, 1992) using the function "pq3.prcomp" in S version 4 (Chambers and Hastie, 1992). Correspondence analysis showed the relations between rows and columns in a frequency table graphically as points in a common low-dimensional space (Clausen, 1998). Both objects (rows) and categories (columns) of variables are represented as points in such a way that an object is relatively close to its category and relatively far from other categories (Leeuw and van Rijckevorsel 1988). For example, the 72nd angler fished 10 days in June, five days in July, seven days in August, three days in September, one day in October, and this angler was mapped closed to June, reflecting the month of his highest fishing effort (Fig. 7). The results suggest several fishing patterns with high catch seasons in June–July, July–

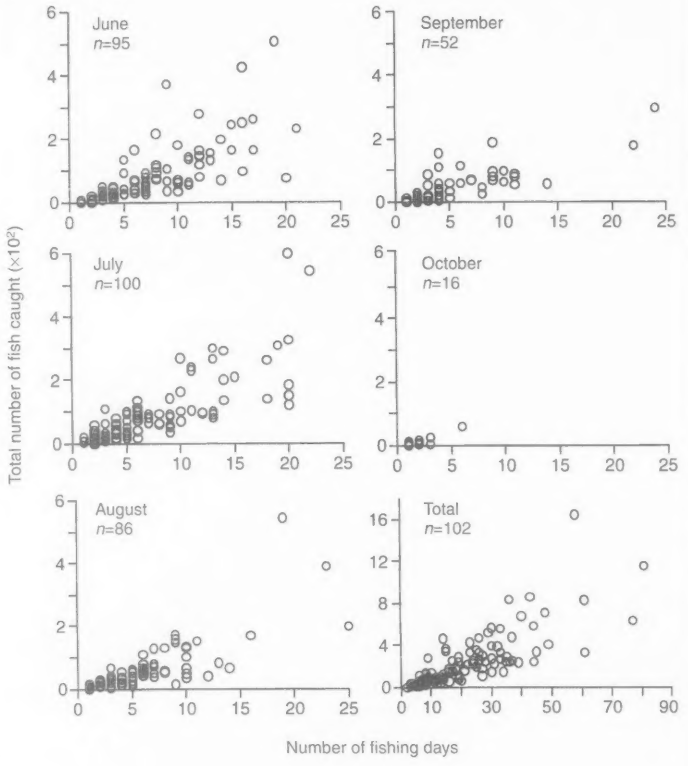

Figure 4

Relationship between the number of fishing days and the number of fish caught by 104 sampled season-permit anglers in the Nakagawa River.

August, August–September, and September–October, resulting high correlations between adjoining months, and large covariances between distant months (Table 4).

The prime advantage of a longitudinal study is its effectiveness for studying change, and a repeated measures analysis of variance can be applied to a complete data set with a constant correlation (Diggle et al., 1994). However, our data set was incomplete because the number of anglers who fish in each month changed (see n in Fig. 4) and had a different correlation structure among month (Table 4). We tested the differences between successive monthly catch estimates of season-permit anglers by using a parametric bootstrapping method. In the central limit theorem, the sample distribution of a monthly total catch estimate can be regarded as a normal with the mean $C_k^{(s)}$ and the variance $\hat{V}(C_k^{(s)})$. Based on the two point estimates, variance estimates and the correlation coefficient between successive two months, we generated 10,000 bivariate normal random variables (Gentle, 1998). The means and 95% confidence intervals of the differences between two monthly total catch estimates were –226,561 [–650,404~203,080] for June and July, 870,720 [455,091~1,277,402] for July and August, 470,594 [161,013~783,168] for August and September, and 537,488 [290,905~782,727] for September and October. Significance levels were corrected for multiple testing by using the Bonferroni ajustment factor (Sokal and Rohlf, 1995).The confidence interval for June and July straddled 0, showing no significant difference. On the other hand, three other confidence intervals did not include 0; therefore the monthly differences were statistically significant (Fig. 8).

Discussion

Bias and source of variation

The estimate of the total annual catch of ayu by the recreational fishery was the first obtained in Japan and was much larger than expected. The total number of day-permits sold was 9066, and was quite small (1.9%) compared with the estimated total number of anglers (477,520).

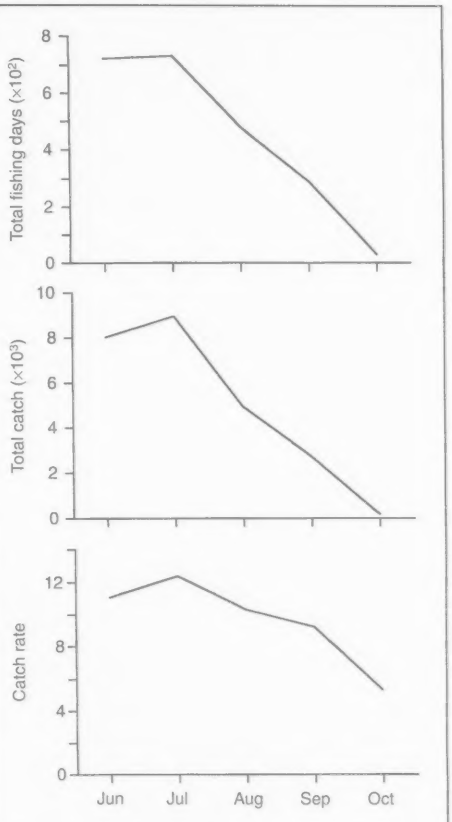

Figure 5

Monthly changes in the number of fishing days, total catch, and catch rate for 104 sampled anglers in the Nakagawa River.

Although the difference in the catch rate between day- and season-permit anglers was unknown, the influence of this bias on the total catch estimates would be minor. In order to check the bias, however, one could conduct a logbook survey of day-permit anglers. Sixteen anglers of the total sample (13%) in our study did not return logbooks and therefore may have caused a bias in our estimates; however no attempt was made to evaluate the difference between nonrespondents and respondents. The angler sample was drawn arbitrarily by the cooperatives but was not a random sample in the strictest sense. If cooperative anglers tended to be selected, this could have been a source of bias.

The source of variation in total catch is the variation in the catch of the sampling unit, including differences in fishing days, skill of the anglers, and the number of anglers that a party boat could accommodate. A stratified sampling scheme based on categories of anglers or boats is effective for this situation. The weakest point in the use of logbook surveys, perhaps, is that the catch data are reported by those who catch the fish and by boat owners with monetary interests. To what extent the anglers might have exaggerated or under-reported their catch is not known. Party boat owners may record lower than actual catches to reduce taxes. To examine this possible source of bias, on-site surveys should be conducted. For the ayu fishery in the Nakagawa River, an access point survey may be practical (Pollock et al., 1994). When comparatively complete lists of boat owners and anglers are available, logbook surveys based on these lists, combined with on-site surveys, are appropriate.

Longitudinal and stratified survey designs

Longitudinal surveys taking repeated measures on the same random sample over time are better than successive independent surveys if the designer's goal is to show statistically significant differences in the estimates between time intervals. Monthly estimates showing seasonal trends

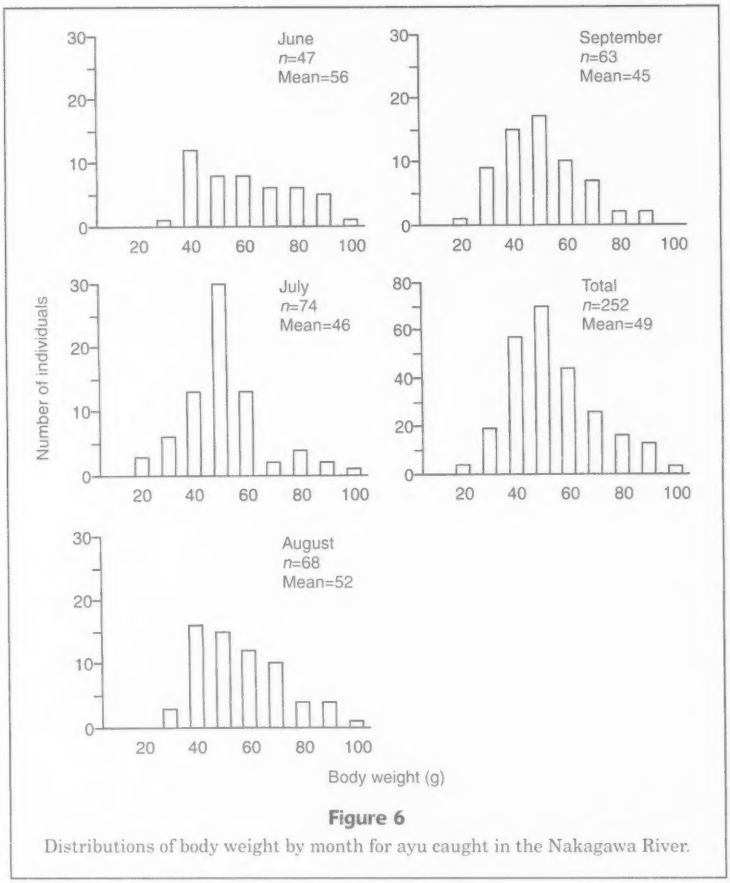

Figure 6

Distributions of body weight by month for ayu caught in the Nakagawa River.

can be obtained by the equations derived in our study. In such repeated measure designs, the most precise estimates of annual catch are obtained by method 2. On the other hand, stratified surveys, or successive independent surveys between time intervals based on random samples of anglers or boats, are better than longitudinal surveys if the designer's goal is to obtain precise estimates of total effort, or catch (or total effort and catch), over the entire season. Stratification by month would improve the precision of annual estimates even more if estimates varied greatly across months. Stratified sampling allows independent monthly estimates, and monthly estimates can be summed to produce precise estimates over time. In the absence of correlations between monthly sample observations, the estimated variance of annual estimates can be obtained simply by adding the estimated variances of the monthly estimates. The estimated variances of annual estimates stratified by month would be considerably less than those of annual estimates based on repeated monthly observations of a one-time annual sample.

If method 2 is used to analyze data obtained by such independent surveys, how would the precision of the estimator compare with the precision of a stratified estimator? For simplicity, we consider a population that is divided into two subpopulations of N_1, N_2 units, respectively. The stratified estimator of the population total and the respective variance are

$$\hat{Y} = N_1\bar{y}_1 + N_2\bar{y}_2,$$
$$\hat{V}(\hat{Y}) = N_1^2\hat{V}(\bar{y}_1) + N_2^2\hat{V}(\bar{y}_2),$$

where $\bar{y}_1$ and $\bar{y}_2$ are the sample means for sample sizes of n_1 and n_2. On the other hand, those obtained by method 2 are

$$\hat{Y}_c = \frac{N_1 + N_2}{n_1 + n_2}(n_1\bar{y}_1 + n_2\bar{y}_2),$$
$$\hat{V}(\hat{Y}_c) = \left\{\frac{n_1(N_1 + N_2)}{n_1 + n_2}\right\}^2\hat{V}(\bar{y}_1) + \left\{\frac{n_2(N_1 + N_2)}{n_1 + n_2}\right\}^2\hat{V}(\bar{y}_2).$$

Subtracting Y_c from Y, we have

Table 2

Estimated parameters and coefficients of variation (in parentheses). $\text{Total}^{\text{meth. 1}}$ = total estimated by summing monthly estimates (method 1). $\text{Total}^{\text{meth. 2}}$ = total estimated by combining data throughout the season (method 2). $R^{(s)}$ = catch rate for season-permit anglers. $\overline{M}$ = mean number of fishing days per season-permit anglers. M_T = total number of fishing days (season+day-permit anglers). $C^{(s)}$ = total catch in number for season-permit anglers. $C^{(d)}$ = total catch in number for day-permit anglers. C = total catch in number (season+day-permit anglers). $W^{(s)}$ = total catch in weight for season-permit anglers. $W^{(d)}$ = total catch in weight for day-permit anglers. W = total catch in weight (season+day-permit anglers).

Parameter	June	July	August	September	October	$\text{Total}^{\text{meth. 1}}$	$\text{Total}^{\text{meth. 2}}$
$R^{(s)}$	11.12	12.37	10.29	9.29	5.35	11.04	11.04
	(0.087)	(0.075)	(0.115)	(0.187)	(1.495)	(0.197)	(0.066)
$\overline{M}$	6.92	7.05	4.62	2.80	0.28	21.66	21.65
	(0.073)	(0.075)	(0.101)	(0.153)	(0.291)	(0.073)	(0.073)
M_T	157,231	157,047	102,722	61,687	6,152	484,839	484,628
	(0.071)	(0.074)	(0.100)	(0.152)	(0.290)	(0.072)	(0.071)
$C^{(s)}$	1,690,440	1,914,495	1,042,772	570,800	32,732	5,251,241	5,251,241
	(0.116)	(0.115)	(0.154)	(0.179)	(0.437)	(0.214)	(0.105)
$C^{(d)}$	57,658	27,915	13,982	2,186	152	101,894	100,108
	(0.087)	(0.077)	(0.118)	(0.197)	(1.528)	(0.056)	(0.066)
C	1,748,099	1,942,410	1,056,755	572,987	32,884	5,353,135	5,351,349
	(0.112)	(0.114)	(0.152)	(0.178)	(0.435)	(0.210)	(0.103)
$W^{(s)}(t)$	94.64	88.30	53.26	25.85	1.48	263.53	253.90
	(0.125)	(0.122)	(0.159)	(0.184)	(0.439)	(0.213)	(0.107)
$W^{(d)}(t)$	3.23	1.29	0.71	0.10	0.01	5.34	4.84
	(0.099)	(0.086)	(0.124)	(0.202)	(1.530)	(0.065)	(0.069)
$W(t)$	97.86	89.59	53.98	25.95	1.49	268.86	258.74
	(0.122)	(0.120)	(0.157)	(0.183)	(0.437)	(0.209)	(0.105)

Table 3

Coefficient of variations of the total catch estimate $\hat{C}^{(s)}$ (method 2) for various sample sizes (number of anglers).

n	CV	n	CV	n	CV
10	0.3401	110	0.1025	230	0.0709
20	0.2405	120	0.0982	250	0.0680
30	0.1963	130	0.0943	300	0.0621
40	0.1700	140	0.0909	400	0.0538
50	0.1521	150	0.0878	500	0.0481
60	0.1388	160	0.0850	600	0.0439
70	0.1285	170	0.0824	700	0.0406
80	0.1202	180	0.0802	800	0.0380
90	0.1134	190	0.0780	900	0.0358
100	0.1075	200	0.0760	1000	0.0340

Table 4

Estimated variance-covariance matrix ($\times 10^{10}$) for the monthly estimates of catch (number) by season-permit anglers in number by Equation 17 (lower diagonal) and the correlation coefficient $r(C_{ik}, C_{ik'})$ (upper diagonal, in bold font). The diagonal component refers to $\hat{V}(\hat{C}_k^{(s)})$ and the lower half refers to $\widehat{\text{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)})$.

Month	Jun	Jul	Aug	Sep	Oct
Jun	3.837	**0.67**	**0.43**	**0.30**	**–0.03**
Jul	6.011	4.862	**0.65**	**0.49**	**0.08**
Aug	9.422	4.434	2.578	**0.65**	**0.28**
Sep	10.681	6.258	1.456	1.038	**0.44**
Oct	10.725	6.336	1.522	0.069	0.020

$$\hat{Y} - \hat{Y}_c = \frac{n_2 N_1 - n_1 N_2}{n_1 + n_2}(\bar{y}_1 - \bar{y}_2).$$

showing that the two methods provide different estimates with the extent of the difference, depending upon the sizes of the strata, the sample sizes, and the estimates of the sample means. According to Cochran (1977), method 2 works well enough if the sample allocation is proportional because a simple random sample distributes itself approximately proportionally among strata. With proportional allocation $N_1/n_1 = N_2/n_2$; therefore the difference of the two estimators is 0. In our case study, the annual

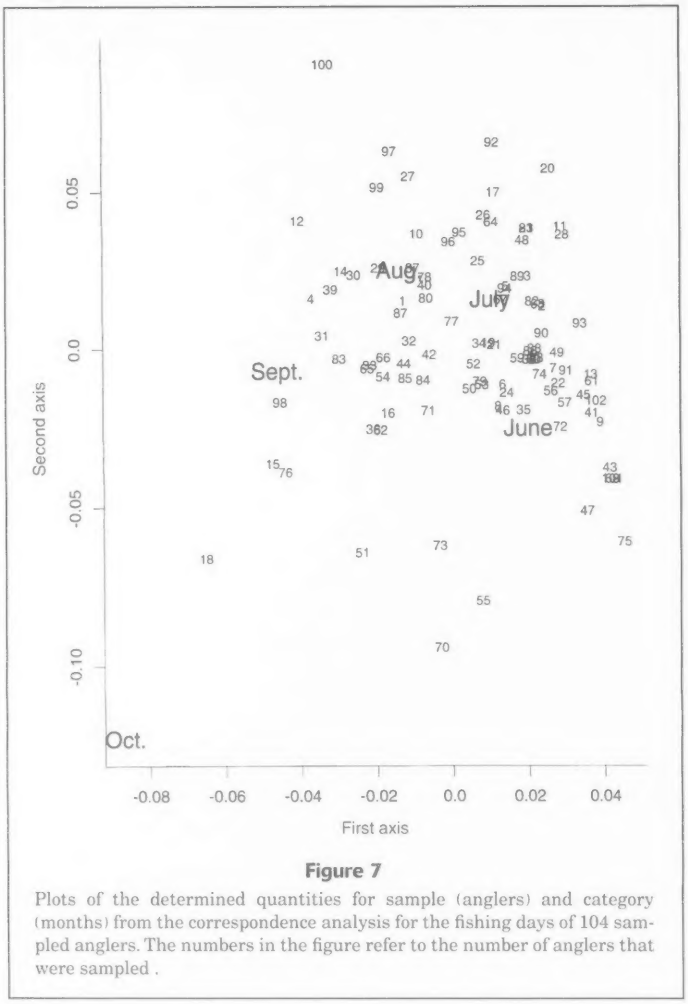

Figure 7

Plots of the determined quantities for sample (anglers) and category (months) from the correspondence analysis for the fishing days of 104 sampled anglers. The numbers in the figure refer to the number of anglers that were sampled .

catch estimates for the season-permit anglers $C^{(s)}$ were the same value for method 1 and method 2. The population size N and the sample size n were in proportion constant throughout the season; therefore $N_i/n_i = N/n$ was same for all strata. The ratio of the variances is

$$\frac{\hat{V}(\hat{Y})}{\hat{V}(\hat{Y}_c)} = \frac{(n_1+n_2)^2\left\{N_1^2\hat{V}(\bar{y}_1)+N_2^2\hat{V}(\bar{y}_2)\right\}}{(N_1+N_2)^2\left\{n_1^2\hat{V}(\bar{y}_1)+n_2^2\hat{V}(\bar{y}_2)\right\}},$$

which also shows that the precision of both methods depends on the sizes of the strata, the sample sizes, and the variance of the sample means. If the allocation is proportional, the variance ratio becomes 1 and the two variances coincide. The objective of stratified surveys is to obtain precise total effort or catch estimates (or both) over the entire season. A proportional sample allocation is recommended, which allows a simple calculation with method 2 and improves precision of estimates at the same time.

Acknowledgements

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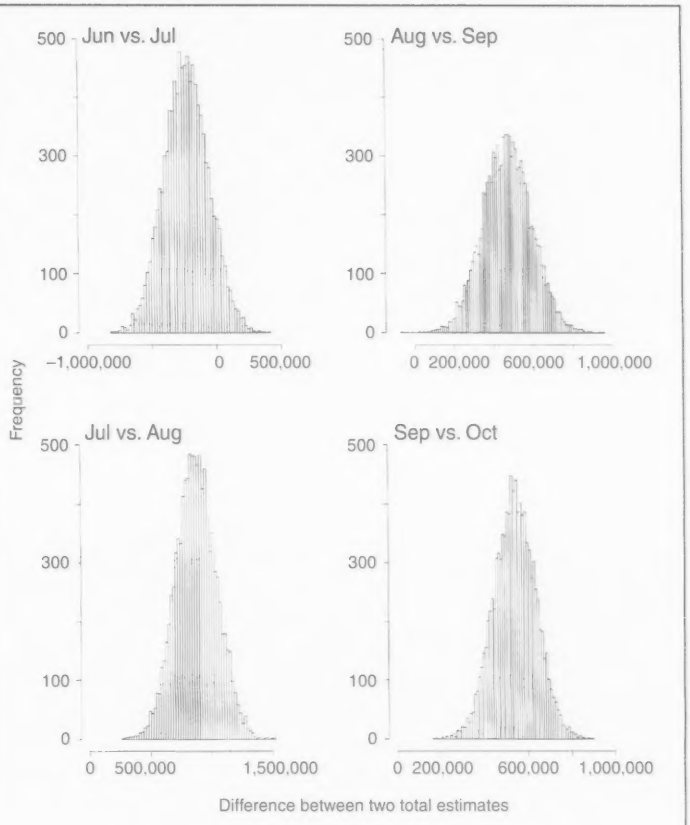

Figure 8

Bootstrap distributions of diffences between successive monthly ayu catch estimates.

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Appendix 1: The covariance of two estimators from sample means

First we consider the covariance of two total estimates. Let X_i and Y_i be simple random samples (i=1, . . . , n) from a population of size N with mean μ_x and μ_y, and $\overline{X}$ and $\overline{Y}$ be two sample means.

Cochran (1977, p .25) derived the covariance of two-sample mean, that is

$$\widehat{\mathrm{Cov}}(\overline{X},\overline{Y}) = \frac{N-n}{N}\frac{1}{n}\widehat{\mathrm{Cov}}(X,Y) = \frac{N-n}{N^2 n}\sum_{i=1}^{N}(X_i-\mu_x)(Y_i-\mu_y).$$

This is estimated by

$$\widehat{\mathrm{Cov}}(\overline{X},\overline{Y}) = \frac{N-n}{N}\frac{1}{n}\widehat{\mathrm{Cov}}(X,Y) = \frac{N-n}{Nn(n-1)}\sum_{i=1}^{n}(X_i-\overline{X})(Y_i-\overline{Y}).$$

The covariance between two population total estimators is defined by

$$\widehat{\mathrm{Cov}}(\hat{X},\hat{Y}) = \widehat{\mathrm{Cov}}(N\overline{X},N\overline{Y}) = E(N\overline{X}-N\mu_x)(N\overline{Y}-N\mu_y) = N^2\widehat{\mathrm{Cov}}(\overline{X},\overline{Y}) = \frac{N(N-n)}{n}\widehat{\mathrm{Cov}}(X,Y).$$

This is estimated by

$$\widehat{\mathrm{Cov}}(\hat{X},\hat{Y}) = \frac{N(N-n)}{n(n-1)}\sum_{i=1}^{n}(X_i-\overline{X})(Y_i-\overline{Y}).$$

For the monthly total catches, we get

$$\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)},\hat{C}_{k'}^{(s)}) = \frac{N(N-n)}{n(n-1)}\sum_{i=1}^{n}(C_{ik}-\hat{\overline{C}}_k)(C_{ik'}-\hat{\overline{C}}_{k'}).$$

Appendix 2: Approximate covariance between $\hat{W}_k^{(s)}$ and $\hat{W}_{k'}^{(s)}$

Taylor's series of $\hat{W}_k$ with respect to the random variables is obtained by

$$\hat{W}_k = C_k\overline{w}_k + \overline{w}_k(\hat{C}_k - C_k) + C_k(\hat{\overline{w}}_k - \overline{w}_k).$$

From Taylor's series (mentioned above), the approximate covariance is obtained.

$$\begin{aligned}\mathrm{Cov}(\hat{W}_k^{(s)},\hat{W}_{k'}^{(s)}) &= E(\hat{W}_k^{(s)}-W_k^{(s)})(\hat{W}_{k'}^{(s)}-W_{k'}^{(s)})\\ &= E\left[\overline{w}_k(\hat{C}_k^{(s)}-C_k^{(s)})+C_k^{(s)}(\hat{\overline{w}}_k-\overline{w}_k)\right]\\ &\quad\left[\overline{w}_{k'}(\hat{C}_{k'}^{(s)}-C_{k'}^{(s)})+C_{k'}^{(s)}(\hat{\overline{w}}_{k'}-\overline{w}_{k'})\right]\\ &= \overline{w}_k\overline{w}_{k'}\mathrm{Cov}(\hat{C}_k^{(s)},\hat{C}_{k'}^{(s)})+\overline{w}_k C_{k'}^{(s)}\mathrm{Cov}(\hat{C}_k^{(s)},\hat{\overline{w}}_{k'})\\ &\quad + C_k^{(s)}\overline{w}_{k'}\mathrm{Cov}(\hat{\overline{w}}_k,\hat{C}_{k'}^{(s)})+C_k^{(s)}C_{k'}^{(s)}\mathrm{Cov}(\hat{\overline{w}}_k,\hat{\overline{w}}_{k'}).\end{aligned}$$

Here $\hat{C}_{(\cdot)}^{(s)}$ and $\hat{\overline{w}}_{(\cdot)}$ are independent, and both w_k and $w_{k'}$ are estimated from different samples. Therefore Cov $(\hat{C}_k^{(s)},\hat{\overline{w}}_{k'}) = \mathrm{Cov}(\hat{\overline{w}}_k,\hat{C}_{k'}^{(s)}) = \mathrm{Cov}(\hat{\overline{w}}_k,\hat{\overline{w}}_{k'}) = 0$, then we get the covariance as only the first term.

Appendix 3: Approximate variance of $\hat{R}$

Taylor's series of $\hat{R}$ with respect to $\hat{C}$ and $\hat{M}$ is obtained by

$$\hat{R} = \frac{C}{M} + \frac{1}{M}(\hat{C}-C) - \frac{C}{M^2}(\hat{M}-M).$$

Then the approximate variance is obtained by

$$V(\hat{R}) = E(\hat{R}-R)^2 = \frac{1}{\hat{M}^2}V(\hat{C}) + \frac{\hat{C}^2}{\hat{M}^4}V(\hat{M}) - 2\frac{\hat{C}}{\hat{M}^3}\mathrm{Cov}(\hat{C},\hat{M}).$$

Appendix 4: Covariance between $\hat{C}_k^{(d)}$ and $\hat{C}_{k'}^{(d)}$

By expanding $\hat{C}_k^{(d)}$ and $\hat{C}_{k'}^{(d)}$ we get

$$\hat{C}_k^{(d)} = Dp_kR_k + DR_k(\hat{p}_k - p_k) + Dp_k(\hat{R}_k - R_k).$$
$$\hat{C}_{k'}^{(d)} = Dp_{k'}R_{k'} + DR_{k'}(\hat{p}_{k'} - p_{k'}) + Dp_{k'}(\hat{R}_{k'} - R_{k'});$$

then the approximate covariance is given by

$$\begin{aligned}\mathrm{Cov}(\hat{C}_k^{(d)},\hat{C}_{k'}^{(d)}) &= E(\hat{C}_k^{(d)} - Dp_kR_k)(\hat{C}_{k'}^{(d)} - Dp_{k'}R_{k'})\\ &= D^2\left[\begin{array}{l}R_kR_{k'}\mathrm{Cov}(\hat{p}_k,\hat{p}_{k'}) + R_kp_{k'}\mathrm{Cov}(\hat{p}_k,\hat{R}_{k'})\\ +p_kR_{k'}\mathrm{Cov}(\hat{R}_k,\hat{p}_{k'}) + p_kp_{k'}\mathrm{Cov}(\hat{R}_k,\hat{R}_{k'})\end{array}\right].\end{aligned}$$

If the first three covariance components are equal to 0 because of independent sampling, then we have

$$\mathrm{Cov}(\hat{C}_k^{(d)},\hat{C}_{k'}^{(d)}) = D^2p_kp_{k'}\mathrm{Cov}(\hat{R}_k,\hat{R}_{k'}).$$

Here we can write $\hat{R}_k$ and $\hat{R}_{k'}$ as the ratio of two random variables from Equation 1 by

$$\hat{R}_k = \frac{\hat{C}_k^{(s)}}{N\hat{\bar{M}}_k}.$$

By using a method similar to that given in Appendix 3, we get

$$\mathrm{Cov}(\hat{R}_k, \hat{R}_{k'}) \simeq \frac{1}{N^4}\left(\begin{array}{l} \dfrac{1}{\hat{\bar{M}}_k\hat{\bar{M}}_{k'}}\mathrm{Cov}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)}) \\ -\dfrac{\hat{C}_{k'}^{(s)}}{\hat{\bar{M}}_k\hat{\bar{M}}_{k'}^2}\mathrm{Cov}(\hat{C}_k^{(s)}, \hat{\bar{M}}_{k'}) \\ -\dfrac{\hat{C}_k^{(s)}}{\hat{\bar{M}}_k^2\hat{\bar{M}}_{k'}}\mathrm{Cov}(\hat{\bar{M}}_k, \hat{C}_{k'}^{(s)}) \\ +\dfrac{\hat{C}_k^{(s)}\hat{C}_{k'}^{(s)}}{\hat{\bar{M}}_k^2\hat{\bar{M}}_{k'}^2}\mathrm{Cov}(\hat{\bar{M}}_k, \hat{\bar{M}}_{k'}) \end{array}\right).$$

Here $\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)})$ and $\widehat{\mathrm{Cov}}(\hat{\bar{M}}_k, \hat{\bar{M}}_{k'})$ are already given by Equation 18 and Equation 24. Hence we can estimate $\mathrm{Cov}(\hat{C}_k^{(s)}, \hat{\bar{M}}_{k'})$ and $\mathrm{Cov}(\hat{\bar{M}}_k, C_{k'}^{(s)})$. These are the covariances between a total estimate and a sample mean. By a method similar to that in Appendix 1, we have

$$\begin{aligned}\mathrm{Cov}(\hat{X}, \bar{Y}) &= E(N\bar{X} - N\mu_x)(\bar{Y} - \mu_y) \\ &= N\mathrm{Cov}(\bar{X}, \bar{Y}) = \frac{N(N-n)}{n}\mathrm{Cov}(X, Y).\end{aligned}$$

The covariance is estimated by

$$\widehat{\mathrm{Cov}}(\hat{X}, \bar{Y}) = \frac{N-n}{n(n-1)}\sum_{i=1}^{n}(X_i - \bar{X})(Y_i - \bar{Y}).$$

For our case, the two covariances are as follows;

$$\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{\bar{M}}_{k'}) = \frac{N-n}{n^2(n-1)}\sum_{i=1}^{n}(C_{ik} - \hat{\bar{C}}_k)(M_{ik'} - \hat{\bar{M}}_{k'})$$

$$\widehat{\mathrm{Cov}}(\hat{\bar{M}}_k, \hat{C}_{k'}^{(s)}) = \frac{N-n}{n^2(n-1)}\sum_{i=1}^{n}(C_{ik'} - \hat{\bar{C}}_{k'})(M_{ik} - \hat{\bar{M}}_k).$$

Physiological ecology of juvenile chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California*

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Abstract–Juvenile chinook salmon, *Oncorhynchus tshawytscha*, from natal streams in California's Central Valley demonstrated little estuarine dependency but grew rapidly once in coastal waters. We collected juvenile chinook salmon at locations spanning the San Francisco Estuary from the western side of the freshwater delta—at the confluence of the Sacramento and San Joaquin Rivers—to the estuary exit at the Golden Gate and in the coastal waters of the Gulf of the Farallones. Juveniles spent about 40 d migrating through the estuary at an estimated rate of 1.6 km/d or faster during their migration season (May and June 1997) toward the ocean. Mean growth in length (0.18 mm/d) and weight (0.02 g/d) was insignificant in young chinook salmon while in the estuary, but estimated daily growth of 0.6 mm/d and 0.5 g/d in the ocean was rapid ($P \leq 0.001$). Condition (K factor) declined in the estuary, but improved markedly in ocean fish. Total body protein, total lipid, triacylglycerols (TAG), polar lipids, cholesterol, and nonesterified fatty acids concentrations did not change in juveniles in the estuary, but total lipid and TAG were depleted in ocean juveniles. As young chinook migrated from freshwater to the ocean, their prey changed progressively in importance from invertebrates to fish larvae. Once in coastal waters, juvenile salmon appear to employ a strategy of rapid growth at the expense of energy reserves to increase survival potential. In 1997, environmental conditions did not impede development: freshwater discharge was above average and water temperatures were only slightly elevated, within the species' tolerance. Data suggest that chinook salmon from California's Central Valley have evolved a strong ecological propensity for a ocean-type life history. But unlike populations in the Pacific Northwest, they show little estuarine dependency and proceed to the ocean to benefit from the upwelling-driven, biologically productive coastal waters.

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Estuaries are considered important in the development of juvenile salmon. In the Pacific Northwest, estuaries have been shown to provide nursery and rearing conditions for juveniles emigrating from streams of birth to the ocean (Reimers, 1973; Healey, 1982; Levy and Northcote, 1982; Myers and Horton, 1982; Simenstad et al., 1982; McCabe et al., 1986). The San Francisco Estuary is the largest estuary on the West Coast and is a segment in the migration corridor for chinook salmon (*Oncorhynchus tshawytscha*) from natal streams in the watersheds of the Sacramento and San Joaquin Rivers, known as California's Central Valley. The Central Valley is unique by having four runs of chinook salmon which constitute a significant socioeconomic resource. Ocean harvest south of Pt. Arena (estimated as 85–95% from Central Valley stocks) and spawning escapement range between 0.5 and 1.3×10^6 chinook salmon per year (1970–98) and represent about $60 million (U.S.) in personal income annually (PFMC[1]). Beyond the direct value of Central Valley chinook salmon, their demography and welfare significantly affect the financial and societal aspects of water rights decisions.

Chinook salmon populations migrating through the San Francisco Estuary are at the southern limit of the species' geographical range and are subject to the impacts of a highly urbanized, industrialized, and agricultural freshwater and estuarine system (Nichols et al., 1986). All chinook salmon runs originating in the Central Valley are in jeopardy. Before 1900, spawning runs were estimated at 2×10^6 adults (Fisher, 1994), but in 1998 only an estimated 0.25×10^6 returned of which about 30% were of hatchery origin (PFMC[1]). The Sacramento River winter-run chinook was the first Pacific salmonid species listed under the U.S. Endangered Species Act of 1973 (ESA). Originally categorized as threatened in 1989, its status was changed to endangered in 1994. Chinook salmon of the Central Valley spring run, once forming the dominant chinook race in California (Clark, 1929), were listed as threatened in 1999. Even the fall run, by far the dominant run today (92% of all Central Valley spawners, 1990–98 [PFMC[1]]), has uncertain status and is an ESA candidate. Hatchery production supports the natural fall run, and the other runs to a much lesser degree. Annually, about 35 million chinook salmon are produced by state and federal hatcheries in the Central Valley; the fall run comprises 95% (Mills et al., 1997).

California and federal water development projects, such as dams and water diversions, have clearly played a role in the decline of Central Valley salmon (Moyle, 1994), but other factors may al-

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[1] PFMC (Pacific Fishery Management Council). 1999. Review of 1998 ocean salmon fisheries. Pacific Fisheries Management Council, Portland, OR, 65 p. PFMC, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201.

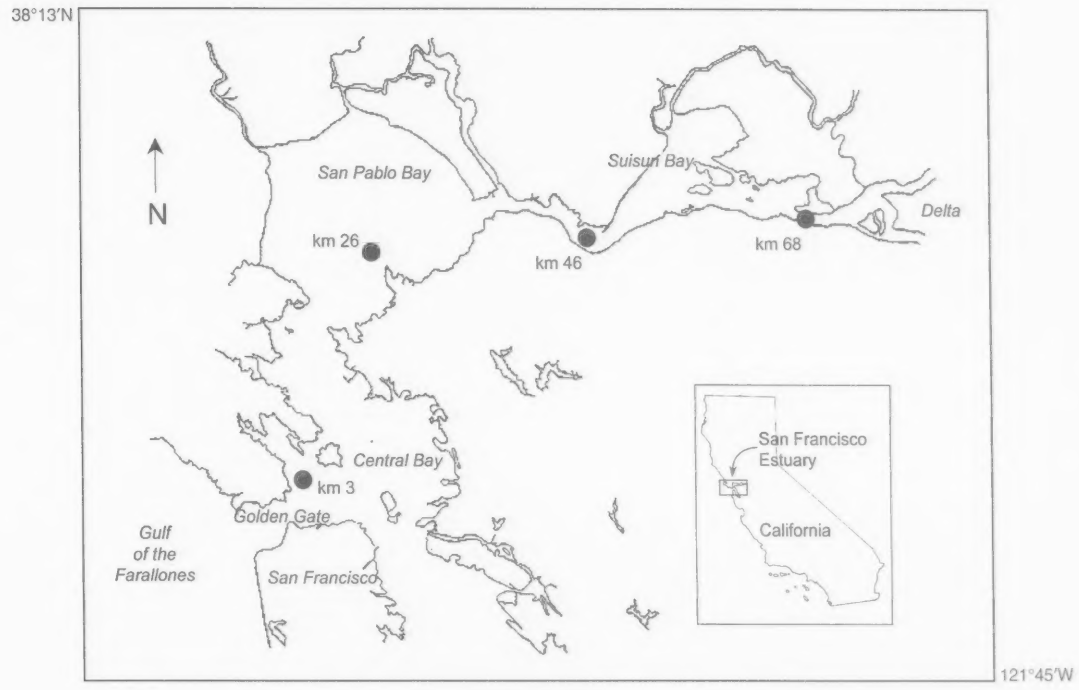

Figure 1

The northern portion of the San Francisco Estuary and nearshore Gulf of the Farallones. Juvenile salmon collection locations are denoted as km (e.g. km 26) from the estuary exit at the Golden Gate. Juvenile salmon were collected throughout the nearshore area in the Gulf of the Farallones, not at specific locations.

so be involved. Migration through the highly impacted San Francisco Estuary and early residence in a marine environment at the southern margin of the species' distribution may impair physiological development that could lead to direct mortality or, indirectly, to reduced survival potential during the oceanic phase.

Although some data exist on abundance, growth, and feeding for chinook salmon migrating through estuaries in southeastern Alaska and British Columbia (Healey, 1980b, 1982; Levy and Northcote, 1982; Landingham et al., 1998); Washington and Oregon (Reimers, 1973; Myers and Horton, 1982; Simenstad, et al. 1982; McCabe et al.,1986; Fisher and Pearcy, 1996); and the Klamath River estuary in northern California (Wallace and Collins, 1997), the only data available for Central Valley emigrants are those of Kjelson et al. (1982). In that paper, life history descriptions were presented for fall-run juveniles, but the emphasis was on fry (≤70 mm fork length) in the freshwater delta at the head of the estuary. Almost nothing is known of juvenile chinook biology in the larger saline portions of the San Francisco Estuary.

Knowledge of juvenile chinook salmon biology during their first year in the marine environment is even more limited, and nonexistent for the area south of the California-Oregon border. Healey (1980a) presented distribution, growth, and feeding information on first ocean-year chinook salmon in the Strait of Georgia, British Columbia. Similar data have been presented for juvenile chinook from the Columbia River drainage off the Oregon and Washington coasts (Miller et al., 1983; Brodeur and Pearcy, 1990; Fisher and Pearcy, 1995).

The purpose of this study was to describe juvenile chinook salmon physiological development during their emigration through the San Francisco Estuary and early residence in the coastal waters of central California. Residence time, age, growth, condition, lipid classes and protein concentrations, and feeding data are presented to characterize the significance of habitat utilization at the southern limit of the species' distribution. The information presented here can serve as a basis for comparison with other year classes from the Central Valley and with populations from more northerly estuaries, as well as for assessments of the influences of natural and anthropogenic perturbations on salmon habitat.

Methods

Study area

Juvenile salmon leaving California's Central Valley pass through the San Francisco Estuary, a series of embayments, before entering the ocean in the Gulf of the Farallones (Fig. 1). The delta, a freshwater network of channels and leveed

islands at the confluence of the Sacramento and San Joaquin Rivers, forms the eastern boundary. Measurable salinity (>1 psu) occurs on the western side of the delta in Suisun Bay. Water flows through Suisun Bay into San Pablo Bay, then into the Central Bay of San Francisco Bay before exiting the estuary at the Golden Gate. The estuary has a surface area of about 1100 km^2 and is fringed on the northern shore with marshes, which have shrunk by more than 90%, to 125 km^2, since 1850 (Conomos, 1979). Most of the estuary shoreline is urban, suburban, and industrial development, however. The Gulf of the Farallones, a relatively broad expanse of the continental shelf extending from Pt. Reyes (38°00′N, 123°01′W) to Pillar Pt. (37°30′N, 122°30′W) to the Farallon Islands (Southeast Farallon Island—37°42′N, 123°00′W) on the edge of the continental shelf, ranges to 90 m but is mostly 20 to 50 m deep. This hydrodynamically complex area is influenced by the cool southerly flowing California Current; freshwater discharge from the San Francisco Estuary; and seasonally strong coastal upwelling (spring and summer) and a northerly flowing countercurrent, the Davidson Current (winter).

Field sampling

Juvenile chinook salmon in this study were collected from the fall run, as determined by the daily length criteria used to discriminate juveniles among the four runs (Johnson et al., 1992). Because salmon from the four runs are phenotypically indistinguishable, to target fall-run juveniles we used daily length criteria and collected fish during the period when fall-run chinook salmon dominate the migration toward the ocean.

We collected juvenile chinook salmon at four locations spanning the San Francisco Estuary (Fig. 1): at km 68, the west side of the delta at the confluence of the Sacramento and San Joaquin Rivers; km 46, the exit from Suisun Bay; km 26 in San Pablo Bay; and several sites within a 1-km radius of km 3 for greater coverage of the estuary exit at the Golden Gate and to avoid ship traffic. Two multiday surveys of the estuary were completed starting at km 68 and proceeding through successive downstream locations to the Golden Gate. The first sampling date was 30 April 1997 at km 68; the last was 15 July 1997 at km 3.

Collections were made in the estuary with a midwater trawl towed at 2–3 knots for 15–30 min. The trawl was made of nylon mesh with a 10-m headrope and footrope, 10-m height at the mouth, and 20-m length. Mesh size was 1.6 cm at the headrope and decreased to 0.4 cm before the codend. The codend was fitted with a 1.27-cm knotless mesh liner. The net was kept open by aluminum spreaders and depressors. For most tows, the spreaders were visible at the surface, confirming that the net fished the upper layer of the water column.

Juvenile chinook salmon were also obtained from the coastal ocean in the Gulf of the Farallones. Stations where salmon were caught were within 15 km of the Golden Gate in waters 18 to 36 m deep. A high-speed midwater rope trawl was towed at 3–4 knots for 15–30 min at each site. The net had a 53-m headrope and footrope with a 1.27-cm mesh codend liner (Dotson and Griffith, 1996). Temperature-depth recorders attached to the footrope and headrope indicated that the net fished 5–10 m below the surface with a vertical opening of 13 m.

Fish were removed from the net as soon as practicable and placed in labeled plastic zip-top bags. Juveniles captured within the estuary were kept under ice: those from the ocean were stored at –80°C, until returned to the laboratory.

We collected hydrologic data during all field trips. Within the estuary, a Hydrolab H20® Multiprobe connected by cable to a Surveyor 3® data logger (Hydrolab Corp., Austin, TX) was used to record vertical profiles of temperature, salinity, dissolved oxygen, pH, and turbidity. In the Gulf of the Farallones, a SeaCat SBE 19-03® (Sea-Bird Electronics, Inc., Bellevue, WA) conductivity-temperature-depth sonde (CTD) recorded profiles of temperature and salinity in a grid of stations spaced at 2′ latitude and longitude intervals encompassing the salmon fishing sites.

Laboratory analyses

In the laboratory, we examined, measured, and dissected fish, usually within 24 h of capture. Fork length and total body weight were recorded. The peritoneal cavity was opened by incision along the ventral side from vent to opercular isthmus. The stomach and its contents were removed and stored in 10% buffered formalin for subsequent analysis of prey. Sagittal otoliths were removed, cleaned of membranes, rinsed in deionized water, and stored for subsequent aging. The remaining portion of the fish was placed in a Whirl® bag, purged with N_2, and stored at –80°C for lipid and protein analyses.

Heads of juvenile salmon containing coded-wire tags, evident by a missing adipose fin, were removed and sent to the U.S. Fish and Wildlife Service, Stockton, CA, to obtain data on the location and time of release of each fish.

Concentrations of lipid classes and total protein were determined in 15 fish randomly chosen from each location. Heads, fins, and stomachs were removed to limit analyses to body constituents. Frozen bodies were minced with a knife, then homogenized in a blender for about 30 sec to a uniform paste. We extracted lipids from a 1g- to 3g-aliquot by using the method of Bligh and Dyer (1959). Total lipid was quantified by thin-layer chromatography with flame-ionization detection with an Iatroscan TH-10 Mark V® (Iatron Laboratories, Inc., Tokyo, Japan) according to procedures published previously (MacFarlane et al., 1990, 1993). Total lipid was separated into steryl or wax ester, triacylglycerols, nonesterified fatty acids, cholesterol, and polar lipid classes and quantified according to methods in MacFarlane and Norton (1999). We estimated total protein concentration by the Lowry method, using bovine serum albumin as a standard (Lowry et al., 1951). All lipid and protein values are expressed as wet weight (mg/g).

Fish ages were estimated from otolith analysis (Brothers, 1987). Sagittae were embedded in epoxy, then ground and polished on the distal surface to a mid-sagittal section. Otolith concentric bands were counted under oil immersion with transmitted polarized light illumination into a video microscopy system at a monitor magnification

of 1500×. Counts representing daily increments of growth were made from the otolith margin (dorsal edge) to a posterior primordium. Each otolith was counted at least two times by the same reader. Data are presented as age, in days, between the hatching check and the otolith margin.

Stomach contents were identified and quantified according to methods of Hobson and Chess (1976). Prey were identified to the lowest possible taxa, enumerated, and their relative volume and size distribution recorded. The derived parameter, index of relative importance (IRI), was used to determine the importance of specific taxa to juvenile salmon at each sampling location. The IRI was computed by the equation

$$IRI = (N + V)FO,$$

where N, V, and FO = the percent number, volume, and frequency of occurrence, respectively, of a taxon in the stomach contents (Pinkas et al., 1971).

Size, age, condition, lipids, and protein data were analyzed for variability among locations by means of the general linear model of analysis of variance. Differences among specific locations were determined with Tukey's studentized range test, set at $\alpha = 0.05$, which controls for MEER (maximum experimentwise error rate) under complete or partial null hypotheses. All statistical procedures were performed with SAS software (SAS Institute, Inc., 1994).

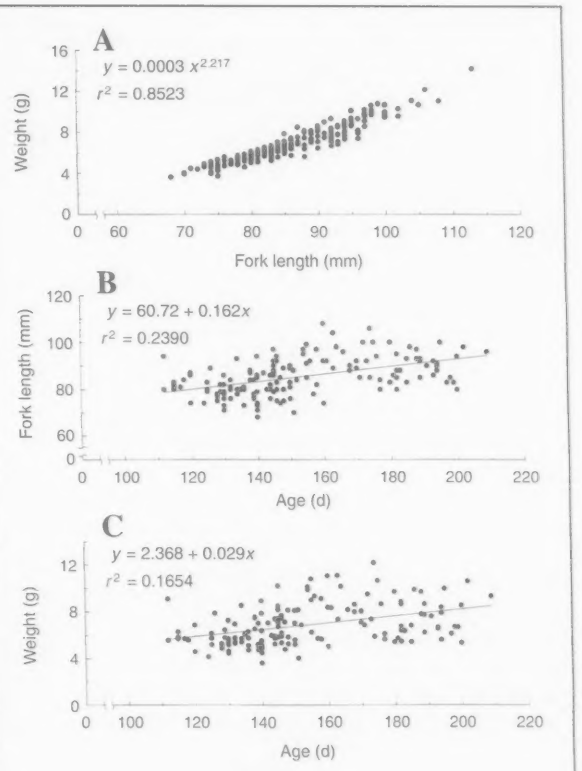

Figure 2

Fork lengths, weights, and ages of all juvenile chinook salmon collected from the San Francisco Estuary and Gulf of the Farallones: (**A**) fork length-weight relationship; (**B**) age-fork length relationship; (**C**) age-weight relationship.

Results

We collected and evaluated 310 subyearling chinook salmon from the 1996–97 year class. The catch consisted of naturally spawned and hatchery-produced fish of unknown proportions because less than 3% were marked (by adipose fin clips and coded wire tags) and there were no morphological features to distinguish hatchery from naturally produced salmon. Mean fork length (FL) was 89 mm and ranged from 68 to 113 mm. Total body weights ranged from 3.59 to 14.62 g, with a mean of 7.58 g. A power function was fitted to the relationship between FL and weight (Fig. 2A). Ages were determined for 156 juveniles and ranged from 112 to 209 days after hatching. The relationship of FL or weight to age was not as well fitted as that for weight on FL (Fig. 2, B and C); however, length and weight were positively correlated to age ($P<0.0001$).

Each sampling location within the estuary was visited more than once on successive surveys through the 30 April–15 July period of juvenile emigration. There were no statistically significant trends in size, age, lipid, and protein variables by sampling date at any location; therefore we combined data for each location from both surveys through the estuary.

While in the estuary, juvenile chinook salmon grew little in length or weight; but in coastal waters, they grew rapidly (Fig. 3). Juveniles entering the estuary at km 68 had a mean (±SE) FL of 82.8 ±0.7 mm and weight of 6.36 ±0.21 g. At the exit of the estuary (km 3), mean FL and weight of cohorts were 89.5 ±1.1 mm and 7.23 ±0.30 g, representing mean gains of about 7 mm and 0.9 g. Size changes within the estuary were not statistically significant ($P>0.05$). Year-class cohorts in the coastal waters of the Gulf of the Farallones were significantly longer and heavier than those from the estuary (FL, $P<0.0001$; weight, $P<0.001$). Ocean-caught juveniles were 8.2 mm longer and weighed 6.5 g more than fish collected near the estuary exit.

Juvenile salmon spent about 40 d migrating along the 65-km length of the estuary, according to otolith increment counts (Fig. 3C). Mean age at the entry to the estuary was 136 ±2 d; at the exit it was 176 ±3 d. Juveniles aged from the Gulf of the Farallones were 156 ±5 days old, indicating a shorter freshwater or estuarine residence than that for those captured from the Golden Gate area.

Daily growth rates in the estuary can be calculated from differences in mean size over the 40-d estimated time of

transit. According to this technique, mean daily growth was about 0.18 mm/d and 0.02 g/d.

Because we aged only a subset of fish from each sampling location, mean age of all fish obtained at each site could be estimated with the FL-on-age regression equation for age (Fig. 2B). Results of that computation revealed close agreement with measured ages at all locations except the Gulf of the Farallones (Fig. 3C), where calculated age was 189 ±8 d. Both methods of age determination indicated that juveniles caught in coastal waters were from the same year class.

The average migration rate through the estuary was estimated at 1.6 km/d on the basis of the difference between mean ages of juvenile salmon sampled at the estuary entry and exit (i.e. 65 km/[176 d at km 3 –136 d at km 68]). Data from coded-wire–tagged fish caught within the estuary and the Gulf of the Farallones revealed a wide range of migration rates (Table 1). For those captured within the estuary (17 of 24), the mean migration rate was 4.0 ±0.9 km/d. Most tagged-recaptured salmon had rates ≤2.6 km/d but were from two releases within the estuary, thus representing migration rates in the lower estuary only. Juveniles released farther upstream in the rivers and caught in the lower estuary had somewhat faster migration rates ($\bar{x}$=9.1 ±2.5 km/d, n= 4).

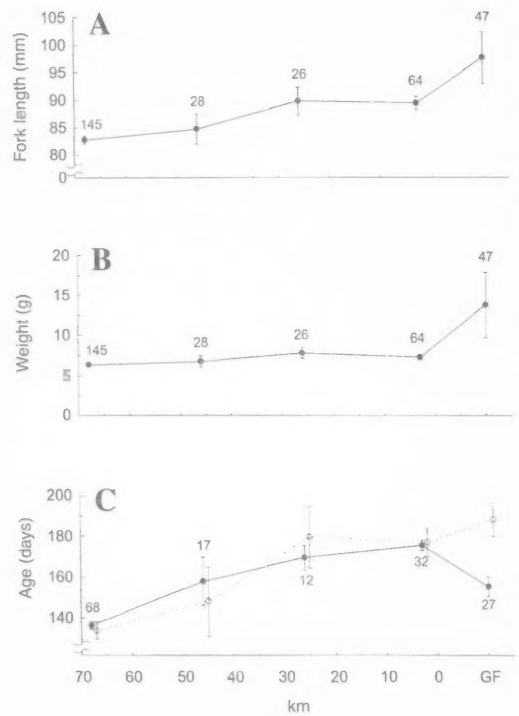

Figure 3

Mean (±SE) fork lengths (**A**), weights (**B**), and ages (**C**) of juvenile chinook salmon collected from locations in the San Francisco Estuary (km 68, km 46, km 26, km 3) and the Gulf of the Farallones (GF). Open circles and dashed line in (C) represent calculated ages of all fish at each location from regression of fork length on age from Figure 2(B). Numbers near means are sample sizes.

Not only did juvenile chinook salmon grow slowly while in the estuary, their condition declined as they proceeded to the Golden Gate (Fig. 4). There was a significant decrease in Fulton's condition factor (K) between fish entering the estuary and those departing (P<0.001). Once the fish were in coastal waters, however, their condition improved markedly.

Body constituents and energy reserves varied little while migrating fish were in the estuary, but total lipid was depleted in fish from the Gulf of the Farallones (Fig. 5A). Total body protein concentrations were approximately 150 mg/g, wet weight, in fish from all locations, and did not vary significantly. Total lipid also did not vary in fish within the estuary but was significantly lower in salmon caught in the ocean (P<0.0005). Mean lipid concentration for fish in the estuary was about 30 mg/g, or 15% of dry weight, and decreased to 17.7 ±1.6 mg/g in the ocean. The decline in lipids in fish from the Gulf of the Farallones was attributed to decreased concentrations of triacylglycerols (TAG), the dominant lipid class (Fig. 5B). TAG levels increased from 14.8 ±2.5 mg/g in fish entering the estuary to about 18 mg/g in estuarine salmon and were depleted to 4.3 ±1.4 mg/g in coastal fish. The concentration of polar lipids, composed primarily of phospholipids, remained unchanged through the estuary and in the ocean. Other lipid classes—cholesterol and nonesterified fatty acids—were found at much lower concentrations and did not vary significantly during the emigration. Steryl or wax esters were absent or at very low levels in most individuals and showed no differences related to location.

We examined feeding and prey selectivity in juvenile chinook salmon migrating through the estuary and in coastal waters. A lesser proportion of fish leaving the rivers contained food items compared with those within the estuary. Fifty percent of juvenile salmon had stomach contents at Chipps Island (km 68, 21 of 42 sampled). In contrast, more than 80% from Carquinez Strait (km 46, 8 of 10 samples) and San Pablo Bay (km 26, 20 of 23 samples) had prey in their stomachs. A lower percentage (70%) from the Central Bay (km 3, 9 of 13) had fed recently, but in the Gulf of the Farallones, 82% (23 of 28) of the juveniles contained food.

The relative importance of prey items varied as juvenile salmon migrated through the estuary and entered the ocean (Table 2). Stomachs of juveniles leaving the rivers contained primarily gammaridean amphipods *Corophium* sp., and lesser amounts of crab megalopae, dipteran insects, other malacostracan crustaceans, and other insects. After the salmon passed through Suisun Bay (km 46), their stomachs contained mostly the hemipteran *Hesperocorixa* sp., the calanoid copepod *Eucalanus californicus*, the mysid *Acanthomysis* sp., fish larvae, and other insects. Cumaceans were clearly dominant in juvenile salmon in San Pablo Bay (km 26), but

Table 1

Minimum distance traveled by coded-wire tagged juvenile chinook salmon between marking and recapture.

Release			Capture					
Date	Location	km	Date	Location	km[1]	Km traveled	Days free	Km/d traveled
1 Apr 1997	Battle Creek	470	12 May 1997	Gulf of Farallones	−19	489	41	11.93
15 Apr 1997	West Sacramento	157	9 May 1997	Gulf of Farallones	−19	176	24	7.33
16 Apr 1997	Battle Creek	470	11 May 1997	Gulf of Farallones	−17	487	25	19.48
24 Apr 1997	Gridley Boat Ramp	244	29 May 1997	Pt. San Pablo	17	227	35	6.49
24 Apr 1997	San Pablo Bay	37	10 May 1997	Gulf of Farallones	−22	59	16	3.69
24 Apr 1997	Gridley Boat Ramp	244	11 May 1997	Gulf of Farallones	−20	264	17	15.53
28 Apr 1997	Mossdale	150	12 May 1997	Gulf of Farallones	−20	170	14	12.14
29 Apr 1997	Dos Reis Park	146	27 May 1997	Carquinez Strait	46	100	28	3.57
29 Apr 1997	Dos Reis Park	146	11 May 1997	Gulf of Farallones	−20	166	12	13.83
14 May 1997	Hatfield State Park	221	29 May 1997	Pt. Pinole	26	195	15	13.00
19 May 1997	Benicia	43	29 May 1997	Pt. Pinole	26	17	10	1.70
19 May 1997	Benicia	43	29 May 1997	Pt. Pinole	26	17	10	1.70
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
30 May 1997	Woodbridge Dam	149	Jun 10 1997	Golden Gate	0	149	11	13.55

[1] Negative km data represent distance captured seaward of the Golden Gate.

insects were still important. In the Central Bay, the final embayment before the estuary exit, fish larvae were the dominant forage item. *Ampelisca abdita*, a gammaridean amphipod, and cumaceans were important as well. Fish larvae continued to be the most important prey of juvenile chinook salmon in the coastal waters of the Gulf of the Farallones, but euphausiids and decapod early life stages were also consumed in significant numbers.

Discussion

Chinook salmon from California's Central Valley streams have a largely ocean-type life history although perhaps a few spring and late-fall run juveniles overwinter in freshwater and migrate to the ocean as yearlings (Fisher, 1994; Myers et al., 1998). Fry (<70 mm FL) are abundant in the freshwater delta from February to April. They leave as smolts (>70 mm FL) and enter the San Francisco Estuary, primarily in May and June. Kjelson et al. (1982) reported that few juveniles were present in the delta or estuary

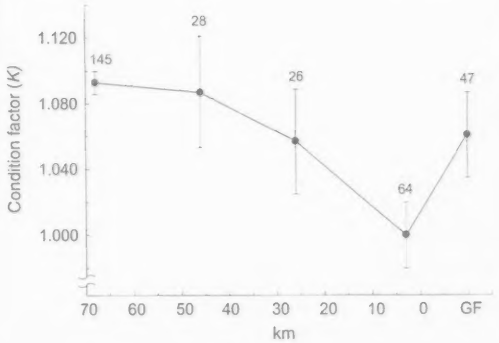

Figure 4

Changes in mean (±SE) Fulton's condition factor (K) of juvenile chinook salmon from locations in the San Francisco Estuary (km 68, km 46, km 26, km 3) and the Gulf of the Farallones (GF). Numbers above means are sample sizes.

after June. Our findings concur: the smallest salmon we caught was 68 mm FL, and we caught no fish after 27 June. Juveniles were approximately 4.5 months old (after hatching) when they entered the San Francisco Estuary. They spent about 40 days there, migrating at 1.6 km/d, based on mean age differences of fish entering the estuary and fish leaving at the Golden Gate. This is probably a minimum estimate of migration rate, because data from tagged fish caught within the estuary showed rates of 1.70 to 13.55 km/d, representing residence times of 38 to 5 days. A previous mark-recapture study also found higher migration rates (10 to 18 km/d), although the data were for passage through the upstream delta (Kjelson et al., 1982).

Studies in the Pacific Northwest suggest that juveniles of ocean-type chinook salmon make extensive use of estuaries, spending as much as 6 to 9 months in them feeding and growing (Myers and Horton, 1982; Simenstad et al., 1982; Healey, 1991). In the Columbia River estuary, subyearling chinook salmon were present throughout the year, although most abundant in May to September (McCabe et al., 1986). Fall-run juveniles entered the Sixes River estuary in the spring and were abundant from June through August (Reimers, 1973). Juvenile chinook salmon resided in Washington estuaries for 6 to more than 29 weeks, but some individuals were present for up to 189 d (Simenstad et al., 1982). Even in northern California's Klamath River estuary, juvenile fall-run chinook salmon remained from June to September (Wallace and Collins, 1997). The relatively short period of abundance in the San Francisco Estuary and emigration rates presented here suggest that juvenile chinook from the Central Valley may derive less benefit from estuarine residence than do more northerly populations.

Juvenile chinook salmon grew little while in the San Francisco Estuary. Though growth was not statistically significant, on average they increased in size by 7 mm FL and 0.9 g, representing daily growth of 0.18 mm/d and 0.02 g/d. These estimates indicate slower growth than has been reported for juvenile chinook in most estuaries to the north. In five estuaries on Vancouver Island and the Fraser River, juveniles grew 0.21 to 0.62 mm/d (Levy and Northcote, 1982; Healey, 1991). Growth measurements from population sampling and from following marked fish produced similar results in the Sixes River estuary, where daily growth ranged from 0.07 mm/d in summer to 0.9 mm/d in spring (Reimers, 1973). Reimers speculated that the very slow growth during summer was due to food limitation caused by high salmon abundance.

Growth can also be inferred by the change in size of fish collected at the same locations from the beginning to the end of the emigration period. We found no significant increase in size at given locations within the estuary during the May–June emigration season. Kjelson et al. (1982) also found no change in smolt size in the delta from April to June. In contrast, the mean size of juvenile chinook salmon in the Columbia River estuary increased from March to December, suggesting substantial growth or immigration of larger fish during the season.

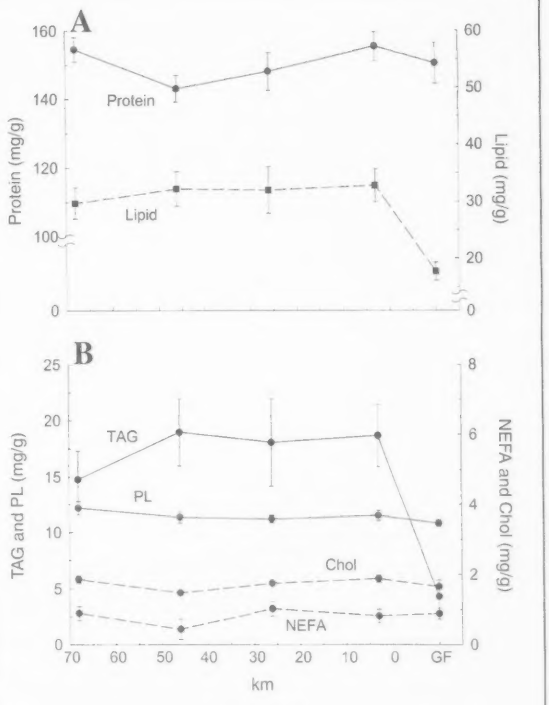

Figure 5

(**A**) Protein and total lipid concentrations, and (**B**) lipid class concentrations (triacylglycerols [TAG], polar lipids [PL], cholesterol [Chol], and nonesterified fatty acids [NEFA]) in juvenile chinook salmon from locations in the San Francisco Estuary (km 68, km 46, km 26, km 3) and the Gulf of the Farallones (GF). Concentrations are mg/g wet weight.

Although little growth occurred during estuarine residence, growth was rapid in the coastal waters of the Gulf of the Farallones. Juvenile ocean cohorts were 10% longer in mean FL and 90% heavier than those from the estuary, although size varied more in ocean residents than in chinook salmon within the estuary. Faster growth rates of juvenile chinook salmon in coastal waters than in estuaries have been reported from British Columbia (Healey, 1980a), and Oregon and Washington (Miller et al., 1983; Fisher and Pearcy, 1995), with rates of 1 mm/d and more. Daily growth rates of juveniles in the Gulf of the Farallones were difficult to determine because the mean age of the subset aged by otolith analysis was less than the mean age of fish at the estuary exit. But if the calculated age of ocean juveniles (from the regression of age on FL) is used, during the calculated 13 d of ocean residence they grew at about 0.6 mm/d and 0.5 g/d, well above rates while in the San Francisco Estuary.

Growth rate estimates from the regressions of FL or weight on age for all juveniles from both the estuary and gulf were 0.16 mm/d and 0.029 g/d. These results agree

Table 2

Stomach contents of juvenile chinook salmon. *%N* is the numerical percentage; *%V* is the percent relative volume; *%FO* is the frequency of occurrence percentage; and *IRI* is the index of relative importance, (*%N* + *%V*)*%FO*.

Location and prey species	*%N*	*%V*	*%FO*	*IRI*
km 68, Chipps Island (*n*=21)				
Malacostraca				
Decapoda				
Caridean shrimp	2.6	5.7	4.8	39.3
Crab megalopae	7.7	10.0	19.0	336.3
Mysidacea				
Unidentified	7.7	4.6	14.3	175.9
Amphipoda				
Gammaridea	2.6	5.7	4.8	39.8
Corophium spp.	30.8	26.4	33.3	1905
Eusirdae unidentified	2.6	5.7	4.8	39.8
Isopoda				
Gnorimosphaero luta	2.6	0.6	4.8	15.4
Insecta				
Hymenoptera				
Unidentified	2.6	5.7	4.8	39.8
Homoptera				
Aphid	2.6	0.3	4.8	13.9
Diptera				
Flies unidentified	2.6	1.1	4.8	17.8
Culicidae	2.6	2.6	4.8	25.0
Unidentified	7.7	6.3	19.0	266.0
Unidentified	10.3	9.7	14.3	286.0
Algae				
Unidentified	5.2	11.4	9.5	157.7
Unidentified	7.7	4.0	4.8	56.2
km 46, Carquinez Strait (*n*=8)				
Malacostraca				
Mysidacea				
Acanthomysis spp.	3.9	17.0	12.5	257.5
Unidentified	2.0	6.0	12.5	100.
Amphipoda				
Gammaridea	3.9	3.0	12.5	86.3
Cumacea	5.9	5.0	12.5	136.3
Copepoda				
Calanoida				
Eucalanus californicus	5.9	15.0	12.5	261.3
Insecta				
Coleoptera				
Unidentified	2.0	14.0	12.5	200.0
Hemiptera				
Hesperocorixa spp.	72.5	1.0	12.5	918.8
Unidentified	2.0	20.0	12.5	275.0
Pisces				
Unidentified	2.9	19.0	12.5	273.8
km 26, San Pablo Bay (*n*=20)				
Crustacean				
Unidentified	—	2.9	5.0	—

Location and prey species	*%N*	*%V*	*%FO*	*IRI*
km 26, San Pablo Bay (*n*=20) *continued*				
Malacostraca				
Decapoda				
Crab megalopae	0.5	0.3	35.0	28.0
Mysidacea				
Unidentified	0.5	0.5	5.0	5.0
Cumacean				
Unidentified	61.7	17.9	50.0	3980
Amphipoda				
Gammaridea				
Ampelisca abdita	1.6	1.2	10.0	28.0
Corophium spp.	3.6	23.2	5.0	134.0
Corophium spinicorne	0.5	4.2	5.0	23.5
Maera spp.	0.5	1.5	5.0	10.0
Unidentified	1.0	1.3	3.6	8.3
Cirripedia				
Thoracic				
Barnacle cirri	1.6	1.3	10.0	29.0
Insecta				
Coleoptera				
Unidentified	1.0	1.1	5.0	10.5
Hemiptera				
Unidentified	0.5	0.5	5.0	5.0
Homoptera				
Flatidae	0.5	0.3	5.0	4.0
Diptera				
Unidentified	1.6	1.0	15.0	39.0
Lepidoptera	1.3	1.0	5.0	11.5
Orthoptera	0.5	0.3	5.0	4.0
Unidentified	10.4	12.7	25.0	577.5
Polychaeta				
Phyllodocida				
Nereidae	1.0	4.7	10.0	57.0
Unidentified	1.6	8.2	15.0	147.0
Pisces				
Unidentified larvae	0.5	2.4	5.0	14.5
Unidentified	0.5	1.6	5.0	10.5
Algae				
Unidentified	8.8	8.7	30.0	10.5
Unidentified	0.5	0.3	5.0	4.0
km 3, Central Bay (*n*=10)				
Crustacean				
Unidentified	—	1.2	10.0	—
Malacostraca				
Decapoda				
Crab megalopae	1.2	0.1	10.0	13.0

continued

Table 2 (continud)

Location and prey species	%N	%V	%FO	IRI
km 3, Central Bay (*n*=10) *continued*				
Cumacean				
Unidentified	45.1	11.1	20.0	1124
Amphipoda				
Gammaridea				
Ampelisca abdita	20.7	8.6	60.0	1758
Copepoda				
Siphonostomatoida	1.2	1.2	10.0	24.0
Cirripedia				
Thoracica				
Barnacle cirri	1.2	1.2	10.0	24.0
Insecta				
Unidentified	8.5	1.2	20.0	194.0
Polychaeta				
Phyllodocida				
Nereidae	1.2	2.5	10.0	37.0
Unidentified	1.2	3.7	10.0	49.0
Pisces				
Unidentified larvae	14.6	55.4	60.0	4200
Unidentified	1.2	10.5	10.0	117.0
Algae				
Unidentified	3.7	3.1	10.0	68.0
Gulf of the Farallones (*n*=23)				
Gastropoda	0.3	0.2	4.3	2.2
Malacostraca				
Decapoda				
Cancer magister (juv)	1.5	6.9	26.0	218.4
Crab megalopae	2.1	7.3	21.7	204.0
Crab zoea	6.8	6.6	26.0	348.4
Caridean shrimp	0.9	1.2	13.0	27.3
Euphausiacea				
Thysanoessa gregaria	6.2	2.6	13.0	114.4
Unidentified	24.9	18.5	47.8	2075
Amphipoda				
Caprella californica	0.3	—	4.3	—
Insecta				
Coleoptera				
Unidentified	0.3	0.3	8.7	5.2
Hymenoptera				
Unidentified	2.1	1.2	8.7	2.3
Homoptera				
Aphid	2.1	0.9	17.4	52.2
Diptera				
Culicidae	0.3	0.1	4.3	1.7
Unidentified	5.3	3.7	21.7	195.3
Arachnida				
Araneae				
Unidentified	0.3	0.2	4.3	2.2
Polychaeta				
Phyllodocida				
Nereidae	0.3	0.5	4.3	3.4
Pisces				
Unidentified larvae	46.3	49.9	70.0	6545

well with growth estimated by differences in mean values at the entrance and exit of the estuary.

Further evidence that residence in the San Francisco Estuary was not beneficial to juvenile salmon was their decline in condition (*K*-factor) while migrating through the estuary. But, along with faster growth, condition improved markedly in juveniles in coastal waters. Changes in *K* can be due to several causes, including stomach fullness and metabolic state. In an associated study of contaminants, the weight of stomach contents was measured at the same locations and dates as the ones described here. Stomach contents were 0.5% ±0.1% of body weight in fish with food in their stomachs at both the entrance and exit of the estuary (MacFarlane, unpubl. data). Further, a greater proportion of fish contained food at the estuary exit, where *K* was the lowest. Thus, differences in stomach fullness were not the cause of lower condition. Changes in metabolic equilibria, reflected in altered body composition of protein and lipids, can change body density, as shown by Brett et al. (1969) for juvenile sockeye salmon (*Oncorhynchus nerka*) and thus affect condition. In juveniles in the San Francisco Estuary, body protein and total lipid concentrations were similar at all sampling locations, so changes in body density were unlikely contributors to reduced condition. However, metabolic costs of smoltification can cause changes in length – weight relationships. During the transformation, salmon can become more slender due to depleted energy reserves (Hoar, 1988), especially TAG (Henderson and Tocher, 1987). It is possible that decreased lipid and protein content, and not changes in relative concentrations, caused by catabolism for seawater adaptation, resulted in juveniles leaving the estuary at a lower weight for a given length than when they first entered. However, in a study conducted in 1999, gill Na^+, K^+-ATPase activity, an indicator of seawater adaptation, was greater in juvenile chinook salmon caught at the entrance to the estuary (km 68) compared with that of those sampled within the rivers leading into the estuary, but was not increased further in those collected at locations within the San Francisco Estuary.[2] This suggests that adaptation was largely completed by the time of estuary entrance and may not be the primary contributor to the body lower condition of fish

[2] Alonzo, J. J., and R. B. MacFarlane. 1999. Unpubl. data. Santa Cruz Laboratory, Southwest Fish. Sci. Ctr. NMFS, NOAA. 110 Shaffer Road, Santa Cruz, CA 95060.

leaving the estuary. Further, Zaugg and McLain (1972) showed that condition was either unchanged or declined for several months after stabilization of higher Na^+, K^+-ATPase levels in salmonids undergoing parr-smolt transformation. The increase in *K*-factor in fish captured in the coastal waters of the Gulf of the Farallones argues against smoltification as the main cause of lower condition in juvenile salmon leaving the estuary.

Although total lipid concentrations were unchanged in juveniles within the estuary, they declined greatly in salmon in the Gulf of the Farallones. Most of the decrease was due to depletion of TAG. It appears that the rapid growth of juveniles in the ocean was fueled by TAG energy reserves acquired during downstream migration. Growth seems to take precedence over maintenance of energy reserves. Increased body lipid (presumably TAG) at the time of ocean entry has been shown to improve juvenile chinook survival (Burrows, 1969; Higgs et al., 1992); thus a lack of substantial TAG accumulation while in the estuary may compromise early ocean survival should prey be scarce.

There was little difference in protein concentrations in juveniles from the estuary and the gulf. This is not surprising: protein appears to be conserved except during periods of starvation. Protein levels in juvenile salmonids have been shown to be unaffected by ration, growth, environmental variation (Shearer et al., 1997; Edsall et al., 1999), or locomotion (Alsop and Wood, 1997).

As juvenile chinook salmon migrated through the San Francisco Estuary, their feeding changed progressively from invertebrates to fish larvae. Young salmon leaving the freshwater delta had recently eaten primarily *Corophium*, which seems also to be a major prey of juvenile chinook in Oregon estuaries (Reimers, 1973; McCabe et al., 1986). In 1979–80, juvenile chinook in the delta preyed primarily on cladocerans and dipterans (Kjelson et al., 1982). Over the past several decades, the zooplankton community in the delta and estuary has changed dramatically because of water diversions and introductions of many exotic species (Kimmerer and Orsi, 1996; Cohen and Carlton, 1998). The change in prey found in our study may be a result of anthropogenic alterations in the ecosystem.

There was greater diversity in feeding in the upper bays—Suisun and San Pablo—where insects, copepods, mysids, and cumaceans formed a major portion of young chinook salmon diet. These embayments are bordered by the last remaining extensive brackish and salt marshes in the northern estuary. Additionally, Suisun Bay includes the mixing zone of fresh and salt water, a well-known locale of high plankton abundance. Thus the high biological productivity of these habitats could be expected to provide diverse food items. The composition of the diet here was similar to that found in more northerly estuaries (Healey, 1991) and provided further evidence that juvenile chinook salmon feed on about the same prey types in these habitats throughout their range.

Chinook salmon are highly piscivorous. Fish larvae were clearly the dominant prey in central San Francisco Bay and in the Gulf of the Farallones. Typically young chinook eat mostly fish larvae as they grow and enter marine environments (McCabe et al., 1986; Fisher and Pearcy, 1996; Landingham et al., 1998). In the coastal waters of the Gulf of the Farallones, juvenile chinook salmon fed on early life stages of euphausiids and decapods as well, but to a lesser extent than on fish. Fish, euphausiids, and decapods were the major prey in coastal ecosystems from Oregon to southeastern Alaska (Brodeur and Pearcy, 1990; Landingham et al., 1998).

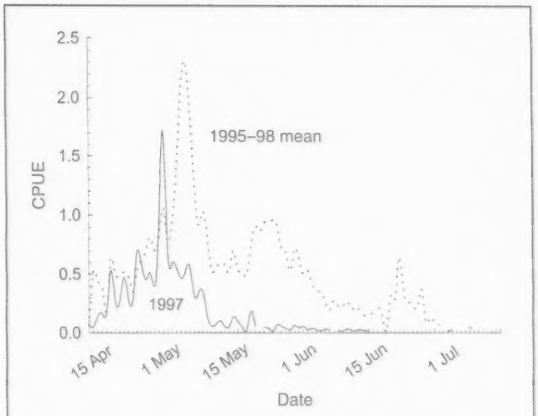

Figure 6

Juvenile chinook salmon catch by midwater trawl at the entrance to the San Francisco Estuary (km 68) in 1997 compared with 1995–98 mean. Catch per unit of effort (CPUE) is presented as the number of salmon/1000 m^3 water. Data from U.S. Fish and Wildlife Service, Stockton, CA.

Once juvenile chinook entered the ocean, feeding intensity appeared to increase. Whereas stomach contents were 0.5% of body weight in the estuary, in the gulf they were 0.9% ±0.1% of body weight. The rapid growth rate found in young salmon shortly after ocean entry seemed to result from greater feeding activity in combination with the utilization of lipid reserves to fuel the synthesis of formed tissues.

To understand the context of data on juvenile salmon physiological ecology, it is helpful to know the relative abundance of these fish and the environmental conditions in 1997. Emigrating juvenile salmon abundance is monitored at the estuary entrance (km 68) by a consortium of California and federal research agencies (Interagency Ecological Program). Data for 1997 indicated that abundance was lower and migration to the ocean occurred earlier than the 1995–98 average (Fig. 6). Mean daily catch per unit of effort (1 January to 30 June 1997) was 0.132 ±0.02 juveniles/(10^3/m^3 water), about 80% less than in 1996 and 1997 and 50% less than in 1998. Freshwater outflow from the delta into the estuary in 1997 was categorized by California Department of Water Resources as "above normal" and peak flows occurred in January, earlier than typical (Fig. 7). Hydrologic conditions in the estuary during May and June 1997 were similar to long-term means, but water temperatures and salinities were statistically higher (P<0.0001, Table 3). Water temperatures were 18.4°C,

Table 3

Mean hydrologic characteristics of the water column in the San Francisco Estuary and the coastal Gulf of the Farallones during juvenile chinook salmon migration toward the ocean in 1997 compared with long-term means. Data are means (±SE) of surface to bottom for May and June. Years for long-term mean were 1989–97, except for turbidity and pH, which were 1995–98. (Long-term data for estuary are from U. S. Geological Survey, Menlo Park, CA, and for gulf from Groundfish Population Analysis, Santa Cruz Laboratory, NMFS, Santa Cruz, CA).NTU = nephelometric turbidity units.

	Estuary		Gulf	
Variable	1997	Long-term	1997	Long-term
Temperature(°C)	18.4 (0.1)[1]	17.5 (0.0)	10.6 (0.0)[1]	10.1 (0.0)
Salinity (‰)	16.7 (0.5)[1]	14.7 (0.2)	33.6 (0.0)	33.6 (0.0)
Dissolved O_2 (mg/L)	7.98 (0.03)[2]	7.91 (0.02)		
Turbidity (NTU)	36.0 (3.0)	35.1 (2.8)		
pH	7.58 (0.01)[1]	7.62 (0.00)		
Chl α (µg/L)	3.19 (0.05)	3.11 (0.03)		

[1] P (probability of no difference from long-term mean) <0.0001.
[2] P<0.05.

about 1°C warmer than long-term means, although well within the tolerance limits for the species at these latitudes (Baker et al., 1995). This temperature has been shown to allow growth rates of about 1% body weight/day in juvenile chinook salmon under simulated field feeding conditions (Weatherley and Gill, 1995).

Water flows and temperature are two primary environmental variables affecting the distribution and development of fishes; thus it is reasonable to assume that the timing of the emigration in 1997 was a function of that year's hydrology. Flow and temperature were believed to influence the migration and distribution of juvenile chinook salmon in the Sacramento and San Joaquin Rivers (Kjelson et al., 1982) and other systems (Cramer and Lichatowich, 1978; Healey, 1980b; Wallace and Collins, 1997). In fact, higher water temperatures of the Central Valley drainage may be a factor in the early emigration and physiological development seen in California chinook salmon in contrast to northerly populations (Healey, 1991). Mean water temperature between 1988 and 1997 at the estuary entrance (km 68) was 19.9°C in June and 21.7°C in July,[3] within the range of predicted 10% mortality estimated with a fitted model (Baker et al., 1995). Temperatures within the Central Bay through July, however, remained below 18°C.

The strongest El Niño of the century began in 1997 and may have influenced the physiology and ecology of salmon in the coastal waters of the Gulf of the Farallones. Water temperatures in the gulf were 0.5°C above the mean for May and June, 1989–97. Although temperatures were within the preferred range for chinook salmon in the ocean (Weatherley and Gill, 1995), altered oceanographic conditions may have changed the composition of the prey community, affecting the feeding of juveniles.

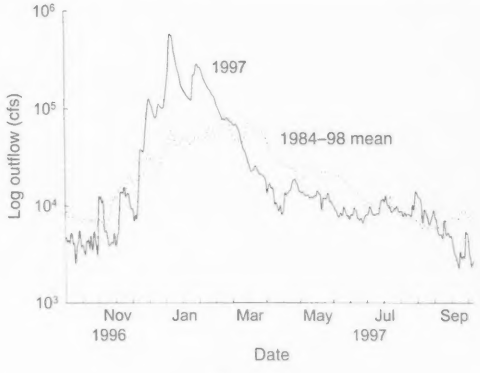

Figure 7

Freshwater outflow into the San Francisco Estuary from the Sacramento River–San Joaquin River Delta in 1997 compared with 1984–98 mean. Outflow data are mean daily cubic feet per second (cfs) from California Department of Water Resources, Sacramento, CA.

Among Pacific salmon, chinook salmon display the greatest variability of life history patterns, including time spent in fresh and brackish water before ocean entry, growth rates, the proportion maturing each year, and fecundity (Healey, 1991). Populations from the Central Valley of California are at the extreme southern end of the species' dis-

[3] Baylosis, J. I., J. L. Edmunds, J. L. Cole, and J. E. Cloern. 1998. Studies of the San Francisco Bay, California estuarine ecosystem: regional monitoring program results, 1997. U. S. Geological Survey Open-File Report 98-168, 194 p. [Available from U. S. Geological Survey, 345 Middlefield Road, Menlo Park, CA 94025.]

tribution and, like many populations at the edges of their distribution, may differ in their early life history from more centrally located stocks. Certainly, Central Valley chinook salmon are known to have unique characteristics such as unusually high fecundity, larger size at age (Healey, 1991), and large population size (PFMC[1]). Lesser estuarine dependence may be another unique trait of these southerly populations. Our data suggest that juvenile chinook salmon derive little benefit from their time spent in the San Francisco Estuary. There was little growth, depleted condition, and no accumulation of lipid energy reserves during the relatively limited time the fish spent transiting the 65-km length of the estuary. Extensive use of estuaries, especially by ocean-type chinook juveniles, seems more typical for populations to the north. Rearing and rapid growth have been characteristic of northerly stocks during extended periods of residence (Reimers, 1973; Healey, 1982; Simenstad et al., 1982; Pearcy, 1992) but were not evident in the San Francisco Estuary (Kjelson et al., 1982; our study).

Emigrating juvenile chinook salmon may not have always used the San Francisco Estuary as they do now. Extensive modification and degradation of the estuary by human activities in the past century or so may have altered the life history pattern of Central Valley chinook salmon populations. Loss of habitat, changes in prey communities, water-flow alterations and reductions, etc. may have contributed to less use of the estuary than previously.

Because Central Valley juvenile chinook salmon exhibit little estuarine dependence, they appear to benefit from expedited ocean entry. The rapid growth seen in the Gulf of the Farallones may confer potential for greater survival. Other chinook salmon studies have determined that larger juveniles are more likely to survive in the ocean (Higgs et al., 1992), leading to higher spawning returns (Burrows, 1969; Reimers, 1973). Faster growth and perhaps greater survival of juvenile chinook salmon, once in the ocean, may be a consequence of a typically favorable and stable thermal environment and the abundant food that results from the high biological productivity of this upwelling-dominated ecosystem (Ainley, 1990; McGowan et al., 1998). The abundant prey resources and lower metabolic costs associated with lower temperatures and ease of obtaining food may improve growth efficiency in the ocean compared with that in the San Francisco Estuary. Reliance on extended freshwater and estuarine residence prior to ocean entry could reduce Central Valley chinook salmon stocks, especially during prolonged periods of drought, which lower freshwater flows and raise temperatures. The ecological and evolutionary propensity of emigrating juveniles to conform to a strong ocean-type life history, with little estuarine dependency and a hastened ocean entry may be another unique attribute of Central Valley chinook salmon populations.

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Bottlenose dolphin (*Tursiops truncatus*) strandings in South Carolina, 1992–1996

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Abstract–From 1992 to 1996, 153 bottlenose dolphin stranded in South Carolina, accounting for 73% of all marine mammal strandings during this period. The objectives of our study were to evaluate data from these strandings to determine 1) annual trends in strandings, 2) seasonal and spatial distribution trends, 3) life history parameters such as sex ratio and age classes, 3) seasonal trends in reproduction, and 4) the extent to which humans have played a role in causing these strandings (human interactions). The results showed that 49% of the bottlenose dolphin strandings occurred between April and July; the greatest number of strandings occurred in July (n=22). There was a significant seasonal increase in the distribution of bottlenose dolphin strandings in the northern portion of the state from November to March. Bottlenose dolphin neonates stranded in every month of the year, except March and October, and represented 19.6% of the total number of strandings with known length (n=138). Fifty-five percent (n=15) of bottlenose dolphin neonatal strandings occurred between May and July. Bottlenose dolphins determined to have died as the result of human interaction accounted for 23.1% of the total number of bottlenose dolphin strandings (excluding those for which a determination could not be made). Incidents of bottlenose dolphin entanglements in nets accounted for 16 of these cases.

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When bottlenose dolphins (*Tursiops truncatus*) began stranding along the South Carolina coast during the 1987–88 die-off, state and federal authorities knew that it was an unusual mortality event. However, since there had been no organized marine mammal stranding network (MMSN) in the state (i.e. without standardized, historical data), the severity of the event could not be evaluated. To avoid this situation in the future, the National Marine Fisheries Service (NMFS) gave the South Carolina Department of Natural Resources (SCDNR) primary authority for the South Carolina Marine Mammal Stranding Network (SCMMSN) in January of 1991. An agreement between NMFS and SCDNR was entered into in 1992 under the Marine Mammal Protection Act (MMPA), and statewide, standardized stranding coverage was begun at that time.

In the epizootic event of 1987–88, it appeared that more than 50% of the migratory population of bottlenose dolphin perished along the eastern United States seaboard (Scott et al.[1]). As a result, the NMFS declared the coastal migratory stock of bottlenose dolphins depleted in 1993 (FR, 1993). Recommendations on data collection were set forth at the Atlantic Bottlenose Dolphin Workshop in Beaufort, North Carolina, 13–14 September 1993 (Wang et al., 1994) for the depleted coastal migratory stock of bottlenose dolphins. As a result, valuable life history data, tissue samples for histopathological and contaminant analyses, and seasonal stranding trends were obtained.

The objectives of this five-year study of stranded bottlenose dolphins in South Carolina were to determine 1) annual trends in strandings, 2) seasonal and spatial distribution trends, 3) life history parameters such as sex ratio and age classes, 3) seasonal trends in reproduction, and 4) the extent to which humans played a role in causing the strandings (human interactions). By examining the stranding data on a finer scale, we would be better prepared to evaluate any future unusual mortality event.

Methods

The South Carolina MMSN is composed of 20–25 people, including volunteers from the general public, university staff, federal, and state agency personnel. A separate group of the network, made up of SCDNR and NOS personnel and local veterinarians, respond to live stranded animals. A 1-800 telephone number, maintained by the SCDNR, receives reports from the public and transfers the information to the network volun-

[1] Scott, G. P., Burn, D. M., and L. J. Hansen. 1988. The dolphin die-off: long-term effects and recovery of the population. Proc. of the Oceans '88 Conf., NY, p. 819–823. Unpubl. manuscript. Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, Florida 33149.

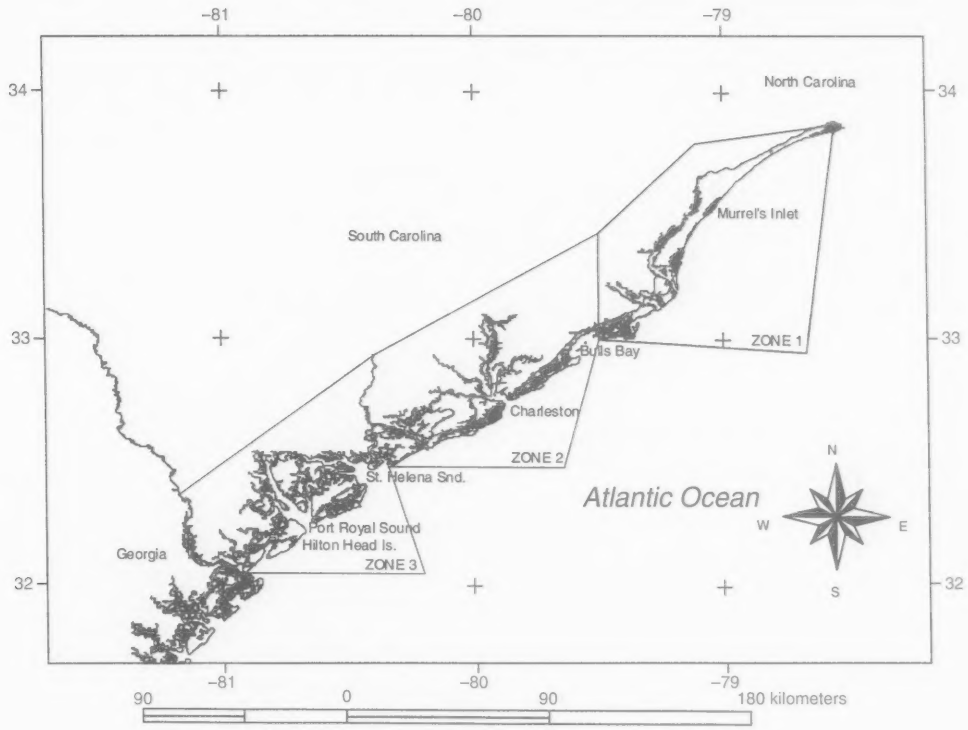

Figure 1

South Carolina coastline showing the three stranding zones: North Carolina border–Bulls Bay (zone 1), Bulls Bay–St. Helena Sound (zone 2), and St. Helena Sound–Georgia border (zone 3).

teers and the state coordinator. Since 1991, the SCDNR has flown the South Carolina coastline from Murrells Inlet to Port Royal Sound (approximately 200 km) once a month to look for stranded marine mammals on remote beaches (Fig. 1). These along-shore surveys were flown in a Cessna 180 high-wing SCDNR plane at 76 m altitude. Aerial reports were also received opportunistically from the U.S. Coast Guard, the Charleston County Sheriff's Department, and SCDNR, and reports were also received from SCDNR scientists (on the ground) who surveyed beaches for sea turtle nesting. Additional strandings were observed during aerial surveys of an investigation into dolphin mortality associated with a coastal shad-net fishery in 1995 (McFee et al., 1996).

For our study, the South Carolina coast was split into three geographical regions based on watersheds and hydrography (Brown, 1977): a northern zone (zone 1) from the North Carolina border to Bulls Bay (approximately 137 km), a central zone (zone 2) from Bulls Bay Island to St. Helena Sound (approximately 100 km), and a southern zone (zone 3) from St. Helena Sound to the Georgia border (approximately 75 km) (Fig. 1). Coverage of the coastline has been consistent since 1992. Although coverage on remote islands was lower in winter and higher in summer, it was constant from year to year. These areas are regularly patrolled by sea turtle personnel from the SCDNR and volunteers, many of whom are also members of the marine mammal stranding network.

Level A data (Hofman, 1991) were collected from each animal. Straight lengths of each bottlenose dolphin were obtained by measuring in centimeters (cm) from the tip of the upper jaw to the fluke notch. Photographs were taken for the majority of animals and were archived at the National Ocean Survey (NOS) Charleston Laboratory. Freshly dead animals were transported to the NOS Charleston Laboratory for necropsy or examined at the site of stranding according to NOS Charleston Laboratory protocol (Galloway and Colbert[2]). Animals in a moderate state of decomposition were not fully examined, but life history samples such as stomachs, ovaries, and skulls were collected. Necropsy reports were catalogued at the NOS Charleston Laboratory.

All stranded marine mammals that were accessible were examined for cause of death or evidence of human interaction (or for both). Stranding network volunteers and

[2] Galloway, S. B., and A. A. Colbert. 1997. Marine forensics manual. Part 1: marine mammals. Unpubl. manuscript. Center for Coastal Environmental Health and Biomoleculer Research, 219 Ft. Johnson Rd., Charleston, South Carolina 29412.

SCDNR personnel were trained to identify characteristic signs of human interaction, such as attached gear, rope or line marks, net marks, propeller cuts, straight-edge knife cuts, puncture wounds, etc. Animals with any of these characteristics were considered to be positive for human interaction. An assessment of stomach contents (full or empty), and histopathology (when available) to determine *ante-* or *post-mortem* injuries were used to corroborate findings. Photographs, and both necropsy and pathology reports from the United States Armed Forces Institute of Pathology (AFIP, Washington, D.C.) also were used to confirm these reports. Those animals that did not show any human interaction characteristics determined with photographs, necropsy, or AFIP pathology reports were considered to have no human interaction. For animals that were too decomposed, not fully examined, examined by untrained personnel, for whom there were inconclusive findings from necropsy or pathology reports, human interactions could not be determined. Therefore, each stranded bottlenose dolphin was classified into one of three categories to determine if human interaction was a possible cause, or contributing factor, in the death of the animals: 1) positive human interaction, 2) no human interaction, and 3) human interaction could not be determined (CBD).

Trends in the stranding data related to year, month, season, gender, and two specific age classes: neonate and females ≥220 cm, were investigated by using chi-square (χ^2) goodness-of-fit and analysis-of-variance (ANOVA) methods. A chi-square test for equal proportions was used to determine if there were differences in the number of strandings between years. An ANOVA was used to determine if there were differences in the number of strandings between months. To determine if there were seasonal trends in the strandings, the data were stratified into groups of three months representing four seasons: January–March (winter), April–June (spring), July–September (summer), and October–December (fall) (Fig. 2). Expected number of strandings for each season was determined by averaging over the 5-year period. To determine whether the stranding pattern for any given year deviated significantly from the "norm," we compared each year's seasonal number of strandings with the expected seasonal number by using a chi-square goodness-of-fit test. An ANOVA was performed to determine if there was a difference in the number of strandings between seasons. A chi-square goodness-of-fit test was used to determine seasonal trends between zones.

A chi-square goodness-of-fit test was used to determine if there was any difference in the proportion of male and female bottlenose dolphin strandings. A chi-square test for trend was used to test the hypothesis that there would be a downward trend in the number of animals that were of unknown sex due to increased training of stranding network volunteers in determining the sex of bottlenose dolphins. A chi-square goodness-of-fit test was used to determine if there was a difference in the number of strandings of females ≥220 cm between seasons.

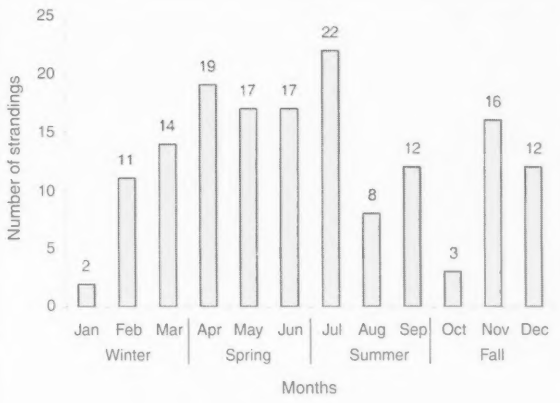

Figure 2

Number of bottlenose dolphin strandings in South Carolina for each month and season of the year from 1992 to 1996 (n=153). The numbers over each bar represent the number of strandings reported for that month.

Results

Yearly trends

From 1992 to 1996, 153 bottlenose dolphin strandings were reported along the coast of South Carolina. The number of strandings each year ranged from a low of 28 in 1992 to 33 in 1993 ($\bar{x}$=30.6) (Table 1); there was no significant difference among years (χ^2 test for equal proportions, P=0.968). Prior to 1992 the highest number of bottlenose dolphin reported stranded for one year was 17 in 1991 (the year the network was formed), excluding the unusual mortality event of 1987 (n=60).

Monthly trends

Over the five-year period, the greatest number of reports (22, or 14.4%) of bottlenose dolphin strandings occurred during July and the least in January (n=2) and October (n=3) (Fig. 2). There was no yearly differences in the total number of strandings by month from 1992 to 1996 (ANOVA, P=0.172).

Seasonal trends

The highest number of strandings occurred in spring (n=53, 34.6%) and the lowest number of strandings were recorded in winter (n=26, 17.0%). Strandings during the years 1992, 1994, 1995, and 1996 did not deviate from the expected pattern (χ^2 goodness-of-fit; P=0.994, 0452, 0.379, and 0.062, respectively), but the seasonal pattern in 1993 was significantly different (P=0.016). This was due in large part to the high number of strandings (n=14) in the fall, when we expected the number to be less than seven.

The ANOVA analysis indicated that the mean number of strandings differs significantly between seasons (P=0.021).

Table 1

Summary of results of human interaction from evaluations of bottlenose dolphins stranded in South Carolina from 1992 to 1996. "Gaff wounds" refer to puncture wounds made by the gaff, a long rigid pole with sharp point(s) used to spear fish or retrieve fishing gear.

	1992	1993	1994	1995	1996	Total
Total dolphins stranded	28	33	31	32	29	153
Human and fishery interactions						
Rope marks	2	0	0	3	4	9
Flukes cut off and mutilations	3	1	1	0	1	6
Boat strike	2	0	1	2	0	5
Blunt-object trauma	0	2	0	1	0	3
Net marks	0	0	0	0	1	1
Gaff wounds	0	1	0	0	0	1
Total	7	4	2	6	6	25
No human interaction	15	21	16	16	15	83
Human interaction could not be determined (CBD)	6	8	13	10	8	45
Percent of human or fishery interaction.[1]	31.8% (n=22)	16.0% (n=25)	11.1% (n=18)	23.1% (n=22)	28.6% (n=21)	27.3% (n=108)

[1] Calculated from total number of strandings minus CBD.

Given that 1993 was an unusual year in the stranding pattern, this year was excluded from the analysis. Specifically, the number of strandings was found to be higher in the spring than in other seasons (contrast analysis, P=0.012).

The majority of strandings occurred in the southern half of the state, zones 2 (n=67; 43.8%) and 3 (n=61; 39.9%). Seasonally, in zone 1 (n=25), 72.0% of its strandings occurred in fall and winter, whereas in zones 2 and 3, the majority of their strandings occurred in spring and summer, 68.7% and 70.5%, respectively. Seventy-three percent (n=11) of the bottlenose dolphins that stranded in the southern half of zone 1 did so between October to April. The difference in seasonal patterns of strandings between zones was significant (χ^2 goodness-of-fit; P=0.003).

Gender

The total number of stranded bottlenose dolphins with known sex was 115. The sex ratio for 1992–96 was 1.00:0.89, females (n=61) to males (n=54), not significantly different from parity (χ^2 test of association; P=0.979). A significant decrease in the proportion of unknown gender occurred during the period 1992–96 (χ^2 test for trend; P=0.012) because of an increase in the number of animals examined in necropsy.

Length classes

The total number of stranded bottlenose dolphins with known length was 138. Based on length-at-age data from known bottlenose dolphins (Read et al., 1993) and stranded bottlenose dolphin data from Texas (Fernandez and Hohn, 1998) the length data were stratified into five classes: class I (neonates—defined as a newborn having a folded dorsal fin or flukes or with umbilical remnants [or with both physical features]); class II (<184 cm, young of the year); class III (185–200 cm—calves); class IV (201–240 cm, mostly physically immature, especially females); and class V (>240 cm, mostly mature) (Fig. 3).

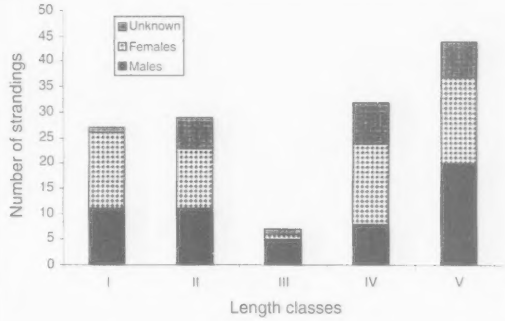

Figure 3

The number of strandings for males, females, and for bottlenose dolphin of unknown sex in each length-class stratum from 1992 to 1996 in South Carolina (class I=neonates; class II≤185 cm; class III=186–200 cm; class IV=201–240 cm; class V≥240 cm).

Males and females were distributed proportionately and evenly across the length classes with the exception of two classes: class III and class IV (Fig. 4). In class III, males

dominated (83.3%). Females were more prevalent in class IV (66.7%). Males showed the lowest numbers of strandings in class III (n=5) and highest numbers in class V (n=20).

Neonates Neonates represented 19.6% (n=27) of the total number (n=138) of strandings of dolphins with known length, ranging from 13.3% in 1993 to 24.1% in 1994 and were found in every month of the year, except March (Fig. 4). Twenty (74.1%) neonates stranded during the spring (n=14) and summer (n=6) months. June had the greatest number of strandings (n=7), followed by May (n=4) and November (n=4). Thirteen of the 27 neonates (48.1%) were <100 cm. Twelve of these stranded during the spring and fall months. More female neonates (1.3:1.0) stranded in South Carolina than males, though this difference was not significant (χ^2 test of association; P=781).

Twenty-four (88.9%) of the neonates stranded in zones 2 (n=13) and 3 (n=11). Neonates were found dead in the inner waterways (n=18) and along the outer beaches (n=9). Twelve of the dead neonates found in the inner waterways were retrieved while they were floating.

Females ≥220 cm Females found at a length that showed them capable of being reproductively mature (i.e. ≥220 cm) (Odell, 1975; Mead and Potter, 1990) represented approximately 50% (n=30) of the total number (n=61) of females stranded. The proportions of females ≥220 cm stranded each year were similar, with the exception of those for 1992, where only one out of seven females was this length. However, this finding may be biased, except for 1994, because of the number of animals ≥220 cm that were of unknown sex. The proportion of strandings of females ≥220 cm in each season was statistically significant (χ^2 goodness-of-fit; P=0.011). A large proportion of the lengths of female bottlenose dolphin stranded during winter (40%) and spring (40%) were ≥220 cm compared with lengths for summer (6.7%) and fall (13.3%).

Human interaction

The total number of stranded bottlenose dolphins where either human interaction or no human interaction could be determined was 108. Twenty-five bottlenose dolphin strandings, averaging five per year, showed evidence of human interaction. Eighty-three showed no signs of human interaction and 45 could not be determined (Table 1). Incidents of net entanglements, made evident by rope or line marks, net (mesh) marks, and mutilations, accounted for 16 of the human interaction cases. Incidence of confirmed human interaction on bottlenose dolphins was highest from March to July (n=18). Rope or line marks were more prevalent from February through May (n=8). The ratio of males (n=10) to females (n=11) was 1:1 in the number of positive human interactions, but there were differences in the length class and types of interaction between the sexes. Of the five males that were involved with net entanglements, four were less than 218 cm. Of the eight females associated with entanglements, seven were greater than 210 cm and six of these were >220 cm. Eighty-eight percent

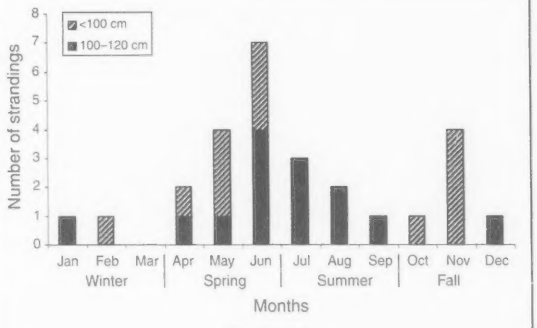

Figure 4

Total number of strandings of neonatal bottlenose dolphins in each month from1992 to1996 (n=27). Diagonally lined boxes represent those neonates <100 cm in length.

of reported human interactions occurred in zones 2 (n=10) and 3 (n=12). Preliminary analysis of stomach contents from bottlenose dolphins stranded on account of human interaction in our study showed that the majority of animals had full stomachs with shrimp or fish remains (or both) (McFee, personal obs.).

Discussion

Despite the establishment of an organized marine mammal stranding network in the southeastern United States since 1990, there has been little published on basic data from stranded bottlenose dolphins other than from reports that can be found as "gray literature." Results from our study indicated the value of analyses of strandings and produced three main findings: 1) the northern portion (zone 1) of the state reported significantly more bottlenose dolphin strandings between November and March 2) neonatal bottlenose dolphin strandings occurred with more frequency between May and July and 3) evidence of human interaction as the cause, or contributing factor, in the deaths of some bottlenose dolphins.

Several hypotheses regarding stock structure of Atlantic bottlenose dolphins have been proposed (Hohn, 1997). One hypothesis is that a single coastal migratory stock migrates seasonally from Long Island, New York, to the central east coast of Florida (Scott et al[3]). The other hypothesis is that multiple bottlenose dolphin stocks exist that include 1) year-round residents with small home ranges, 2) seasonal residents with large home ranges, or 3) migratory groups with long-range movements (Hohn, 1997).

Bottlenose dolphins begin to leave Virginia in mid-October and are mostly absent by mid-November (Swingle,

[3] Scott, G. P., D. M. Burn, and L. J. Hansen. 1988. The dolphin die-off: long-term effects and recovery of the population. Proc. of the Oceans '88 Conf., NY, p. 819–823. Unpubl. manuscript. Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, Florida 33149.

1994; Barco et al., 1999). At about the same time, large numbers of dolphins begin to appear along the "Grand Strand" in northern South Carolina (zone 1) in October and peak in early November, according to bottlenose dolphin sighting data collected during photo-identification studies (Young[4]). During the 1987 bottlenose dolphin die-off, 52 bottlenose dolphin strandings were reported in South Carolina from October through December (Wang et al., 1994). Densities of bottlenose dolphins during a one-year aerial survey of waters from the shore to the Gulf Stream showed the greatest numbers of sightings in fall 1982 (concentrated in the Carolinas), and in winter 1983 (concentrated in northern Florida) (Wang et al., 1994).

Stranding patterns may reflect the abundance of animals. Although large numbers of dolphins occur year-round in South Carolina, there appears to be a peak in strandings in the late fall (November) which would coincide with data from Myrtle Beach (Young[4]), Charleston (Zolman, 1996), and Hilton Head Island (Petricig, 1994) in which greatest abundance of dolphins occurred in late fall. Water temperature, distribution of prey, and use of coastal shrimp trawlers have been implicated as reasons for dolphin movements and abundance in certain areas (Kenney, 1990; Mead and Potter, 1990; Bräger et al., 1994; Fertl, 1994). The late fall increase in the number of strandings in South Carolina could be due to the increased numbers of dolphins from any one of the migratory stocks suggested in the above hypotheses. Zone 1, in particular, provided evidence that a portion of the strandings is from a coastal bottlenose dolphin migratory stock or stocks. The northern half of zone 1 is known as the "Grand Strand" which extends from N. Myrtle Beach to Murrells Inlet (approximately 59 km). This area is highly populated and animals coming ashore here are found and reported regardless of the season of the year. Coverage in the southern half of zone 1 (approximately 78 km) tends to be high from May to September when the beaches are monitored for sea turtle nesting and hatching, but low during October to April. However, the majority of strandings occurred during the latter time period. This may suggest an influx of bottlenose dolphins migrating through zone 1 from October to April, either from the north or south.

We would expect bottlenose dolphin mortality to be similar to that for terrestrial mammals (Ralls et al., 1980): high neonatal and first-year mortality and high adult mortality, and an even distribution of mortality among males and females. If stranding data reflect natural mortality patterns, our results and other studies (Hersh and Duffield, 1990; Hersh et al., 1990; Wells and Scott, 1990; Fernandez and Hohn, 1998) are consistent with mortality patterns suggested for terrestrial mammals. Further, the percentage of stranded bottlenose dolphin neonates (19.6%) was intermediate when compared with that of previous studies (observations in Sarasota, Florida, 36.8% [Wells and Scott, 1990], and Indian/Banana River System, Florida, 11.2% [Hersh et al, 1990]), but similar to that of Texas (20.0% [Fernandez and Hohn, 1998]). We can only assume that mortality during the first year of life is high for bottlenose dolphins regardless of geographical location.

Age and ovarian analysis of stranded bottlenose dolphins ≥220 cm (Odell, 1975; Mead and Potter, 1990) are necessary to determine whether these animals are sexually mature and whether the seasonal patterns noted above correlated with a seasonal reproductive cycle. Seasonal reproduction cycles are complex and not well studied in the South Carolina bottlenose dolphin population but have been demonstrated where adaptations to local environmental conditions may influence seasonal reproductive cycles (Urian et al., 1996).

Over large geographic regions, bottlenose dolphins exhibit year-round calving cycles, but within small geographic regions there may be a higher degree of local reproductive seasonality (Urian et al., 1996). A unimodal seasonal distribution of neonate bottlenose dolphin strandings was noted from Sarasota, Florida, and along the Texas coast, although peak neonatal strandings occurred in different months of the year—May and March, respectively (Urian et al., 1996; Fernandez and Hohn, 1998). A bimodal seasonal distribution was noted for the east coast of Florida in the Indian River Lagoon (Urian et al., 1996). In Sarasota, Florida births have been noted in every month of the year (Urian et al., 1996). Although sample size over the five-year period for our study was too small to estimate significance of trends, our results showed a unimodal distribution and a peak number in June. However, more data may show a bimodal distribution of bottlenose dolphin neonatal strandings because of a second peak that occurred in November. These peaks do not appear to be a function of effort because the majority of neonate strandings occurred on the banks of inland waterways or the neonates were found as floating bodies. The number of neonates in the Stono River estuary, Charleston, South Carolina, peaked in the fall, during a 15-month photo-identification study (Zolman, 1996). Further, all four neonate bottlenose dolphins stranded in South Carolina in November were <100 cm; therefore these animals may have been aborted near-term fetuses.

The determination of human interaction as the cause of mortality for bottlenose dolphins is an important role of the marine mammal stranding networks and can influence management decisions. For example, the Marine Mammal Protection Act (MMPA), as amended in 1994, required that annual stock assessment reports for each stock of marine mammals be prepared. One of the items to be addressed in these reports was a description of commercial fisheries that interact with each stock and the level of mortality caused on each stock by each fishery (Waring et al., 1999). The level of mortality each fishery contributes to a stock, in turn, is essential in determining potential biological removal (PBR) estimates for the stock and the subsequent classification category that regulates each fishery (Waring et al., 1999). The current PBR for Atlantic coastal bottlenose dolphins is 25 (Waring et al., 1999). In a study on the American shad (*Alosa sapidissima*) fishery in South Carolina from 1994 to 1995, no human interactions were shown to be a cause of bottlenose dolphin mortality in the area of fishery effort (McFee et

[4] Young, R. 1998. Personal commun. Coastal Carolina University, P.O. Box 1954, Conway, SC 29526.

al., 1996). As a result, the South Carolina shad fishery retained its original classification as a category-III fishery (i.e.unlikely to take marine mammals in the course of operation) as described in the MMPA amendments of 1988.

Bottlenose dolphin mortality due to human interactions is variable along the eastern United States and Gulf of Mexico (Wang et al., 1994). Incidents of human interaction in South Carolina were also variable over our five-year study period. We believe that the number of bottlenose dolphins in our study showing positive human interaction is a minimum because determination of human interaction cases is difficult to assess owing to a lack of trained personnel, the decomposition of some carcasses, and the presumption that some interactions do not leave any physical evidence. It was a rare occurrence to have gear attached to the carcass; therefore, determination of human interaction was usually made by observing external marks such as cross-hatched lines or lines imprinted by the fishing gear. Human interaction as a cause or contributing factor in a dolphin's death can include fishery interactions (crab pots, trawls, etc.), boat collisions, gun shot wounds, environmental contaminants (agricultural run-off, pesticide use, oil spills). These interactions can result in acute (drowning in a net) or chronic (environmental contaminants) death, show physical evidence (net marks) on the body or none at all.

The percentage of human interaction cases observed in South Carolina was low compared with those in North Carolina strandings (>35% in some years; Wang et al., 1994; FR, 1997). Resident bottlenose dolphins in South Carolina appear to be exposed to different fishing operations than do bottlenose dolphins that migrate through or inhabit North Carolina waters. Net marks were the most common observation (10.5 animals per year) of human interaction cases in North Carolina (FR, 1997), whereas in South Carolina only one presumed net-caught animal was observed over a five-year period. In South Carolina incidents of entanglements as evidenced by rope or line marks are puzzling. At this time, it is highly speculative as to which fishery in South Carolina may be responsible for the incidence of entanglements associated with rope or line marks.

There is evidence to suggest that relationships exist between gender and lengths of various species of cetaceans involved with human interaction (Perrin et al., 1994; Cox et al., 1998). In our study small male bottlenose dolphins and female bottlenose dolphins ≥220 cm showed evidence that they were subject to human interaction. One study found that females with calves spent more time feeding at shrimp boats than did lone animals (Fertl, 1994). Food intake for lactating females can increase dramatically (Cockroft and Ross, 1990). Although heavy-feeding behavior may be energetically beneficial, it may also be costly to both the calf and mother by exposing them to fishing gear and predation.

In summary, the stranding data collected for bottlenose dolphins in South Carolina from 1992 to 1996 provides baseline information for the demographics, life history studies, and management concerns for comparing future stranding rates of bottlenose dolphins in South Carolina. Although it cannot be definitively stated that stranding rates coincide with a portion of a migratory stock, strandings in the northern portion (zone 1) do increase during a period of greater dolphin abundance. More years of data will further elucidate the seasonal reproduction distribution for bottlenose dolphin. Finally, the detection of human interaction as a cause or contributing factor in the deaths of some bottlenose dolphins in South Carolina has demonstrated the need to continue the effort to report these incidents for management purposes.

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Validated age and growth of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean

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Abstract–Growth parameters were estimated for porbeagle shark (*Lamna nasus*) in the northwest Atlantic Ocean on the basis of vertebral annuli. A total of 578 vertebrae was analyzed. Annuli were validated up to an age of 11 years by using vertebrae from recaptured oxytetracycline-injected and known-age sharks. Males and females grew at similar rates until the size of male sexual maturity, after which the relative growth of the males declined. The growth rate of the females declined in a similar manner at the onset of maturity. Growth curves were consistent with those derived from tag-recapture analyses (GROTAG) of 76 recaptured fish and those based on length-frequency methods with measurements from 13,589 individuals. Von Bertalanffy growth curve parameters (combined sexes) were L_∞ = 289.4 cm fork length, K = 0.07 and t_0 = –6.06. Maximum age, based on vertebral band pair counts, was 25 and 24 years for males and females, respectively. Longevity calculations, however, indicated a maximum age of 45 to 46 years in an unfished population.

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The porbeagle (*Lamna nasus*) is a large pelagic shark in the family Lamnidae that occurs in the cold, temperate waters of the North Atlantic, South Atlantic, and South Pacific oceans. The species extends from Newfoundland to New Jersey in the western North Atlantic (Castro, 1983), and from Iceland and the western Barents Sea to Morocco and the Mediterranean in the eastern North Atlantic (Compagno, 1984). Directed commercial fisheries for porbeagle have existed in the western North Atlantic in both U.S. and Canadian waters since the early 1960s (Campana et al.[1]). The fishery collapsed in 1967, apparently from overfishing. Canadian fishermen maintained low and apparently sustainable catches in the 1970s and 1980s, which allowed the stock to rebuild. A renewed fishery for porbeagle began in both the United States and Canada in the 1990s (Campana et al.[1]).

Accurate age determinations are necessary for both the assessment and management of the porbeagle shark because they form the basis for calculations of growth and mortality rates, age at maturity, age at recruitment, and estimates of longevity. Aasen (1963), in an early study of porbeagle growth, generated a growth curve for the western North Atlantic population based on analyses of length frequencies from a single year and on vertebral readings of one fish. However, he did not provide any independent confirmation of the accuracy of his age estimates. Francis and Stevens (2000) used length-frequency analysis to estimate the growth of juvenile porbeagles in the South Pacific. Both of these studies indicated that porbeagle grow relatively rapidly through the first year of life, but only minimal information has been available for older fish.

In view of the history of the porbeagle fishery and the need for accurate biological information for management of this species, an intensive U.S.-Canadian cooperative research program was initiated in 1999 to obtain detailed life-history and population data. This study reports on one portion of this program, specifically, the use of vertebrae to determine age and growth. The vertebral growth readings were validated as annuli on the basis of recaptures of tetracycline-injected and known-age sharks and verified by comparison with growth curves based on tag-recapture and length-frequency analyses.

[1] Campana, S., W. Joyce, L. Marks, P. Hurley, L. J. Natanson, N. E. Kohler, C. F. Jensen, J. J. Mello, and H. L. Pratt Jr. 2000. The rise and fall (again) of the porbeagle shark population in the Northwest Atlantic. Unpubl. manuscr. Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

Materials and methods

Vertebral aging

Vertebral samples from porbeagle sharks were obtained between 1966 and 1999 on board commercial and research vessels. The majority of samples (97%) were collected after 1990 on Canadian commercial longline vessels. Sampling took place in U.S. and Canadian waters between Massachusetts (NE U.S.) and the Grand Banks (off southern Newfoundland) and all individuals were treated as belonging to the same stock on the basis of tagging data (Campana et al.[2]). Multiple vertebrae were removed from the area just above the branchial chamber wherever possible; except on commercial vessels where samples were obtained closer to the head. Vertebrae were then stored frozen or in 70% ETOH until processing.

Only samples that had measured fork length (FL—tip of the snout to the fork in the tail, over the body) or total length (TL—tip of the snout to a point on the horizontal axis intersecting a perpendicular line extending downward from the tip of the upper caudal lobe to form a right angle, over the body; Kohler et al., 1995) were used. All lengths reported in this document are over-the-body FL unless otherwise noted. Total length in centimeters (cm) can be converted to FL cm by using the regression equation (Campana et al.[1]):

$$FL = 0.885(TL) + 0.99 \qquad [n = 361\ r^2 = 0.99].$$

One vertebra from each sample was removed for processing. The centrum was sectioned by using a Ray Tech Gem saw with two diamond blades separated by a 0.6-mm spacer. Each centrum was cut through the middle along the sagittal plane and the resulting "bow-tie" sections were stored individually in capsules in 70% ETOH. Each section was digitally photographed with a MTI CCD 72 video camera attached to a SZX9 Olympus stereo microscope by using reflected light. Magnification depended on the size of the section and varied from 4× to 12.5×. Band pairs (consisting of one opaque and one translucent band) were counted and measured from the images by using Image Pro 4 software (Media Cybernetics, 1998). Measurements were made from the midpoint of the isthmus of the full bow-tie to the middle of the opaque growth bands at points along the internal edge of the corpus calcareum (Fig. 1). The vertebral radius (VR) of each centrum was measured from the midpoint of the isthmus to the distal margin of the intermedialia along the same diagonal as the band measurements.

The identity of the birth band in the vertebra was confirmed through comparison of the birth band radius (BR) measurements to vertebral radius measurements of late-term embryos, early young-of-the-year, and late age-0 fish. The late-term embryo vertebral samples were obtained from the South Pacific porbeagle population, courtesy of Malcolm Francis.[3] The assumptions were made that vertebral growth *in utero* was comparable between the two populations and that measurements of the rehydrated dried South Pacific vertebrae were similar to those from wet NW Atlantic preparations.

The relationship between VR and FL was calculated in order to confirm the interpretation of the birth band and to determine the best method for back-calculation of size-at-age data. The FL to VR relationship was curvilinear; therefore, the data were ln-transformed before linear regression. The Fraser-Lee equation of the ln-transformed data was derived for back calculation:

$$\frac{\ln(FL_a) = b + (\ln[FL_c] - b)(\ln radius_a)}{(\ln radius_c)}$$

where a = age;
b = intercept from the FL-VR regression; and
c = capture.

Validation

The accuracy of the vertebral band pair counts as annual indicators was determined by using both known-age recaptures and recaptures of oxytetracycline (OTC)-injected and tagged individuals. Vertebrae from young of the year (YOY) sharks whose FL was measured at both tagging and recapture were used for known-age analyses. Band pair counts were compared with time at liberty to determine band pair periodicity. One hundred and fifty-five porbeagles of various lengths were also tagged and injected with 25 mg/kg of OTC (senior author, unpubl. data) Returned vertebrae from these sharks were examined with reflected UV light for the OTC mark. The number of band pairs distal to the OTC mark were then compared with the number of years at liberty.

Data analysis

Aging bias and precision of annulus counts were examined by using age-bias plots and the coefficient of variation (Campana et al., 1995). Two readers independently counted 100 vertebral sections from which the pair-wise age-reader comparisons were generated.

Von Bertalanffy growth functions (VBGF) were fitted to the length-at-age data by using the following equation (von Bertalanffy, 1938):

$$L_t = L_\infty(1 - e^{-K(t-t_0)}),$$

where L_t = predicted length (cm) at age t;
L_∞ = mean theoretical maximum fork length;
K = a growth rate parameter (per yr); and
t_0 = the theoretical age (yr) at zero length.

[2] Campana, S., L. Marks, W. Joyce, P. Hurley, M. Showell, D. Kulka. 1999. An analytical assessment of the porbeagle shark (*Lamna nasus*) population in the northwest Atlantic. Canadian Stock Assessment Secretariat Research Document 99/158, 57 p. Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

[3] Francis, M. 2000. Personal commun. National Institute of Water and Atmospheric Research P.O. Box 14-901, Wellington, New Zealand.

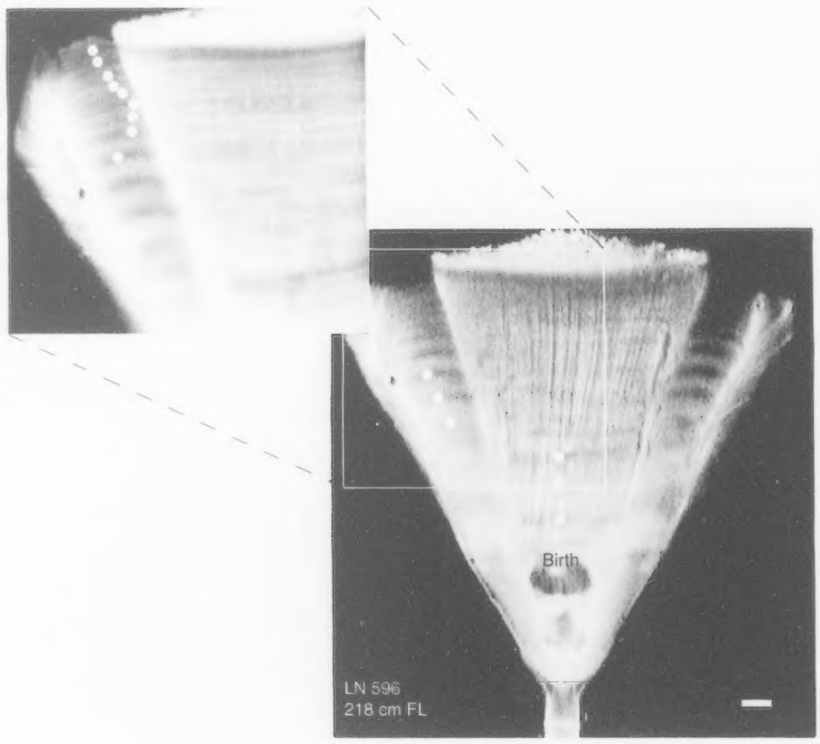

Figure 1

Photograph of a vertebral section from a porbeagle estimated to be 15+ years old. Insert shows higher magnification view of narrow bands at edge. Scale bar = 1 mm. White dots are on annuli.

The VBGF was calculated by using the nonlinear regression function in Statgraphics. Locally weighted least squares regression (LOESS) curves were fitted to the FL vs. age data for each sex by using Statgraphics (Manguistics, 1997).

Length frequency

Length-frequency data were obtained from the Canadian International Observer Program operating primarily on the Scotian Shelf, and some data from the Grand Banks. Although the entire data set (1986–98) was analyzed, only data from the most complete year (1991) were used for the final analysis.

Monthly length-frequency histograms were developed for eight months of 1991 for modal analysis. Calculations of mean fork length and annual growth rate for ages 0 and 1 were based on the first two modes of these data, which were easily distinguished and tracked across months.

MULTIFAN (Fournier et al., 1990) was used to estimate the VBGF parameters from the 1991 length-frequency data. The model analyzes multiple length-frequency distributions by using a maximum likelihood method to estimate the number of age classes present and VBGF parameters L_∞ and K. An initial systematic search was conducted based on user-supplied K values and age classes. Constraints were placed on the estimates of length at age for the first two age classes. MULTIFAN allows the user to start with a generalized search and then add parameters to further refine the model. The initial search included estimates of K ranging from 0.05 to 0.25 and age classes of 11 through 20. The hypotheses tested were the following: 1) constant length standard deviation for all age classes; 2) variable length standard deviation for all age classes; 3) constant length standard deviation for all age classes with seasonal growth; and 4) variable length standard deviation for all age classes with seasonal growth. A model incorporating constant length standard deviation was fitted first with the additional parameters added sequentially. Results from the four models were compared by using log-likelihood tests following Fournier et al. (1990) and Francis et al. (1999).

The von Bertalanffy growth parameter t_0 was estimated from the equation

$$t_0 = t_1 - a_1, \quad (1)$$

where a_1 = the age estimated by MULTIFAN for the youngest age class at the time it first appeared in the length-frequency samples; and
t_1 = the time elapsed in years between the theoretical birthday and the first appearance of the youngest year class in the samples.

The theoretical birthday was defined as 1 April based on the gestation period and the time of mating (Jensen et al.[4]). The first appearance of the youngest age class in the samples was 1 July.

The model with seasonal growth components required the use of a modified von Bertalanffy equation to incorporate the amplitude and phase of the seasonal growth:

$$L_t = L_\infty\left(1 - e^{\left(-K\left(t - t_0 + (\phi/2\pi)\sin\left(2\pi((12t+1)/12) - \phi_2\right)\right)\right)}\right), \quad (2)$$

where ϕ_1 = amplitude; and
ϕ_2 = (MULTIFAN phase) + t_1 (from Eq. 1).

Tag-Recapture analysis

Data from three independent tagging studies from the western North Atlantic Ocean were combined for tag and recapture analysis. In the 1960s, 542 porbeagles were tagged and 53 recaptured as part of a Norwegian study of the unfished population. In 1994 through 1996, the Canadian Department of Fisheries and Oceans (DFO) conducted a tagging program in which 256 porbeagles were tagged and 25 recaptured. Between 1979 and 1999, members of the National Marine Fisheries Service's (NMFS) Cooperative Shark Tagging Program tagged 1034 and recaptured 119 porbeagles. Sharks were tagged and recaptured by biologists and commercial and recreational fishermen in the United States and Canada and by biologists in the Norwegian study. All measurements were converted to FL by using the morphometric conversions reported in Campana.[1] Where Norwegian measurements were reported as Aasen's (1963) total length, they were converted to FL with the equation:

$$FL = 0.93TL.$$

Only those sharks reliably measured at the time of tagging and recapture were used in the analyses. Reliability was based on prior knowledge of the individual's expertise in measuring the shark or on detailed questioning of those individuals as to the method used. The majority of sharks were measured by NMFS biologists or their representatives.

The Gulland and Holt (1959) and Francis (1988a) models were used to generate VBGFs from the tag-recapture data. The Gulland and Holt (1959) method uses graphical interpretation of the recapture data to produce estimates of L_∞ and K. Specifically, annual growth rate (cm/yr) was plotted against average FL (cm) between tagging and recapture to calculate linear regression coefficients. The slope of the line is equal to $-K$ and the x-axis intercept is equal to L_∞.

The Francis (1988a) method (GROTAG) uses maximum likelihood techniques to estimate growth parameters and variability from tagging data. With this method, a coefficient of variation of growth variability (v), the mean and standard deviation of measurement errors (m and s), and outlier contamination (p), are estimated as well as growth rates at two user-selected lengths (α and β). The reference lengths, α and β, were chosen to lie within the range of tagged individuals. The form of the von Bertalanffy equation becomes

$$\Delta L = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_1\right]\left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta}\right)^{\Delta T}\right], \quad (3)$$

where L_1 = length at tagging;
ΔL and ΔT = increments in length and time, respecitively; and
g_α and g_β = mean annual growth rates at the arbitrary lengths α and β.

The simplest model, with minimal parameters (α and β), was used initially with additional parameters added to successively increase model complexity. Significant improvement in the model results were determined by using log likelihood ratio tests (Francis, 1988a). The modeling was carried out by using a Solver-based spreadsheet in MS Excel (Simpfendorfer[5]).

The value of t_0 cannot be estimated from tagging data alone; rather it requires an estimate of absolute size at age, such as size at birth, and was calculated with the VBGF by solving for t_0 such that

$$t_0 = t + (1/K)\left[\ln\left\{(L_\infty - L_t)/L_\infty\right\}\right], \quad (4)$$

where L_t = known length at age (size at birth);

The t_0 values were calculated from an average size at birth of 67 FL cm (Aasen, 1963) with $t = 0$.

Longevity

Several methods were used to estimate longevity. The oldest fish aged from the vertebral method provides an initial value, but is likely to be underestimated in a fished population. Taylor (1958) defined the life span of a teleost species as the time required to attain 95% of

[4] Jensen, C., L. J. Natanson, H. L. Pratt Jr., N. E. Kohler, and S. Campana. 2001. The reproductive biology of the porbeagle shark, *Lamna nasus*, in the western North Atlantic Ocean. Unpubl. manuscript. Apex Predators Program, NMFS, 28 Tarzwell Dr., Narragansett, RI 02882.

[5] Simpfendorfer, C. 2000. Unpubl. data. Mote Marine Laboratory, 1600 City Island Park, Sarasota, FL 33577.

the L_∞. Using a wide range of species, Hoenig (1983) calculated the relationship between longevity, t_{max}, and the natural mortality rate, M, needed to attain one percent of initial abundance in an unfished population as

$$\ln(M) = 1.44 - 0.982 \ln(t_{max}).$$

However, a relationship based on other species need not be used (Campana et al.[2]). Assuming a constant instantaneous natural mortality, M, in an unfished population, the following equation applies:

$$\text{Ln (proportion of fish that survive to age } t_{max}) = -Mt_{max}.$$

As with Hoenig (1983), this equation was evaluated at a value of 0.01 for the proportion of fish that survive.

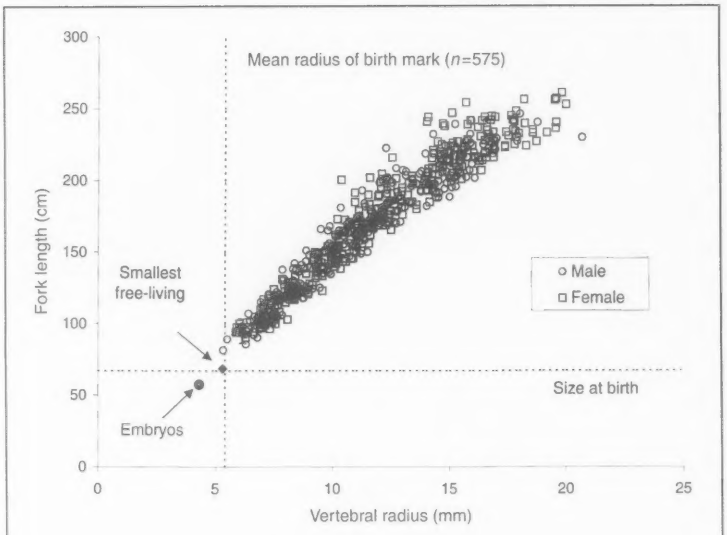

Figure 2

Relationship between vertebral radius and fork length for male and female porbeagles. The solid diamond is the mean vertebral radius of the smallest free-living specimens (n=2), the solid circle is the mean vertebral radius of the largest embryos (n=3). The horizontal line represents the size at birth and the vertical line represents the mean radius of the birth mark in sharks less than 150 cm FL.

Results

Vertebral aging

Vertebral samples from 578 porbeagles were used in our analysis; 283 were males, 292 were females, and 3 were of unknown sex. All vertebrae had distinct band-pair patterns (Fig. 1). The birth mark was indicated by a slight change in angle of the centra and was often the most pronounced first band pair. Subsequent annuli consisted of a pair of alternating opaque and translucent bands that crossed the entire centrum, except in the oldest sharks. Band-pair width decreased with age, narrowing substantially in the oldest individuals (Fig.1).

The FL-VR relationship was curvilinear (Fig. 2), and although the ln-transformed relationship was not completely linear, it was preferable. Therefore, regressions were calculated based on the ln(FL)-ln(VR) relationship where

$$\ln(\text{FL}) = 0.88 \times \ln(\text{VR}) + 2.96 \qquad [r^2=0.94, n=575].$$

There was no significant difference between the regressions of males and females (ANCOVA, P>0.01).

The identity and location of the birth band was confirmed through comparison of the BR of all individuals to the VR of YOY and embryos. The mean VR of three late-term embryos ranging in size from 56.1 to 58 cm FL (mean VR=4.3 mm, CI=0.57) was slightly less than the mean BR value of the total sample (mean BR=5.4 mm, CI=0.03 mm, n=578). The mean BR those of two early YOY (67.7 and 69.2 cm FL) were also similar to those of the total sample (mean VR=5.3 mm, CI=1.27 mm). The VR of the age-0 individuals ranging in size from 76.5 to 100 cm FL (mean VR=6.2 mm, CI=0.31 mm, n=16) was slightly higher (Fig. 2). The placement of the mean BR between the VR of both the YOY and embryos indicates that the birth ring was identified correctly. The birth ring radius increased slightly with increasing FL likely because of an increase in the length of the isthmus of the bow-tie section in larger sharks.

Validation

Known-age recaptured porbeagles and OTC-injected recaptured porbeagles returned with vertebrae confirmed the accuracy of the band-pair counts as indicators of age. Six porbeagles tagged as YOY were recaptured after three to five years at liberty (Table 1). Of the four sharks that were recaptured in the spring, all had translucent material at their growing edge. In contrast, the two sharks recaptured in November had a broad opaque zone at the growing edge. In each case, the vertebral band-pair counts matched the expected counts based on time at liberty (Fig. 3). Vertebrae from six OTC-injected sharks were returned after 0.02 to 2.5 years at liberty. All vertebrae showed a distinct fluorescent mark indicating that the OTC was incorporated within six days (0.02 years) of injection (Fig. 3). Two of the OTC-injected sharks were at liberty for over one year and were used for validation. In both cases, the expected number of growth bands was deposited on the vertebrae between the date of injection and the date of recapture (Table 1). The shark at liberty for 2.5 years had 3 full bands after the OTC mark, the last band having formed just prior to capture. The OTC-injected shark at liberty for 1.5 years was an adult (189.8 cm FL) at tagging and was aged, by vertebrae, to be 11 years at recapture. This

Table 1

Tag-recapture data for the OTC-injected and known-age recaptured porbeagles with vertebrae. TFL = fork length at tagging, RFL = fork length at recapture.

	Sample number	Sex	TFL (cm)	RFL (cm)	Date tagged	Date recaptured	Years at liberty	Growth (cm)	No. of bands past birth mark
Known age	LN 207	F	104.0	178.0	10 Nov 1993	23 Apr 1999	5.4	74.0	6
	553	M	85.0	160.0	1 Nov 1994	9 Nov 1999	5.2	75.0	5
	206	M	100.0	153.0	24 Oct 1994	27 May 1999	4.6	53.0	4
	556	F	97.0	154.0	17 Nov 1995	19 Nov 1999	4.0	57.0	4
	185	F	89.7	148.5	17 Nov 1995	29 Mar 1999	3.4	58.8	4
	183	F	94.2	145.0	17 Nov 1995	23 Mar 1999	3.3	50.8	4
									No. of bands past OTC mark
OTC-injected	LN 171	M	118.0	156.0	16 Sep 1996	30 Mar 1999	2.5	38.0	3
	172	M	189.8	187.0	27 Sep 1997	29 Mar 1999	1.5	–2.8	1+
	473	F	104.0	117.0	15 Apr 1999	21 Nov 1999	0.6	13.0	—
	184	M	147.5	152.0	21 Oct 1998	30 Mar 1999	0.4	4.5	—
	204	M	105.0	95.0	23 Mar 1999	23 May 1999	0.2	–10.0	—
	173	F	96.5	96.0	26 Sep 1997	2 Oct 1997	0.02	–0.5	—

shark had one full band and 83% growth of the next band, based on the size of the last full band. This, along with the YOY known-age individuals, confirmed annulus formation and our band interpretation from birth to 11 years of age. Sharks older than age 11 were assumed to have been aged correctly due to a similar interpretation of the bands.

Data analysis

Comparisons of counts between the two readers indicated no appreciable bias (Fig. 4). The coefficient of variation for age 1+ sharks was approximately 15%. In the absence of bias, this level of precision was considered acceptable; thus the counts generated by one reader for the entire set of vertebrae were used for the analyses.

Length-at-age data showed that males and females grow at similar rates until approximately 170 cm FL, at which point the relative growth rate of the males declines (Fig. 5). The change in relative growth between the sexes coincides with the size and age of male maturity (Jensen et al.[4]). Von Bertalanffy growth functions fitted to the vertebral band-pair count data suggested that males attain a smaller maximum size than females (Table 2). The growth rate of females also declined at size at maturity (approximately 218 cm FL; Jensen et al.[4]). The considerable overlap in size at age between the sexes indicated that the difference in growth rate is minor; therefore subsequent comparisons were made for the sexes combined.

Tag-Recapture analysis

A total of 76 porbeagles was recaptured with sufficient information for tag-recapture analysis. Time at liberty ranged from 0.02 to 6.0 years and size at tagging ranged from 78 to 204 cm FL. Sharks were tagged and recaptured in all months of the year. Tagging effort was fairly evenly distributed throughout all months, whereas most recaptures were made between March and May (53%). For both tagging and recapture, January and February were represented by the least data (3% and 1% for tagging and recapture, respectively). More tags were released in December than were recaptured (12% of the tags but only 2% of the recaptures). Most tagged sharks were small (74% <150 cm FL) because the majority were opportunistically tagged onboard commercial fishing vessels. Data from 54 sharks at liberty greater than 0.9 years were used in the Gulland and Holt (1959) analysis, whereas all individuals were used for GROTAG (Francis 1988a).

The results of the likelihood ratio tests with GROTAG (Francis, 1988a) demonstrated that the more complex nonlinear model with five of the six parameters included was the best fit for these data (model 3, Table 3). The high value of s suggests a lack of sufficient information for GROTAG (Francis, 1988a) to distinguish between growth variability and measurement variability (Francis and Mulligan, 1998). The mean annual growth rates at FL= 95 cm and 150 cm were 19.21 cm/yr and 9.52 cm/yr, respectively (Fig. 6). Von Bertalanffy estimates from the Gulland and Holt (1959) and GROTAG (Francis, 1988a) methods produced similar results (Tables 2 and 4).

Length frequency

Analysis of modal length-frequency progressions verified the size at age and growth rate of age-0 and age-1 individuals (Fig. 7). Age-0 fish entered the fishery in July with

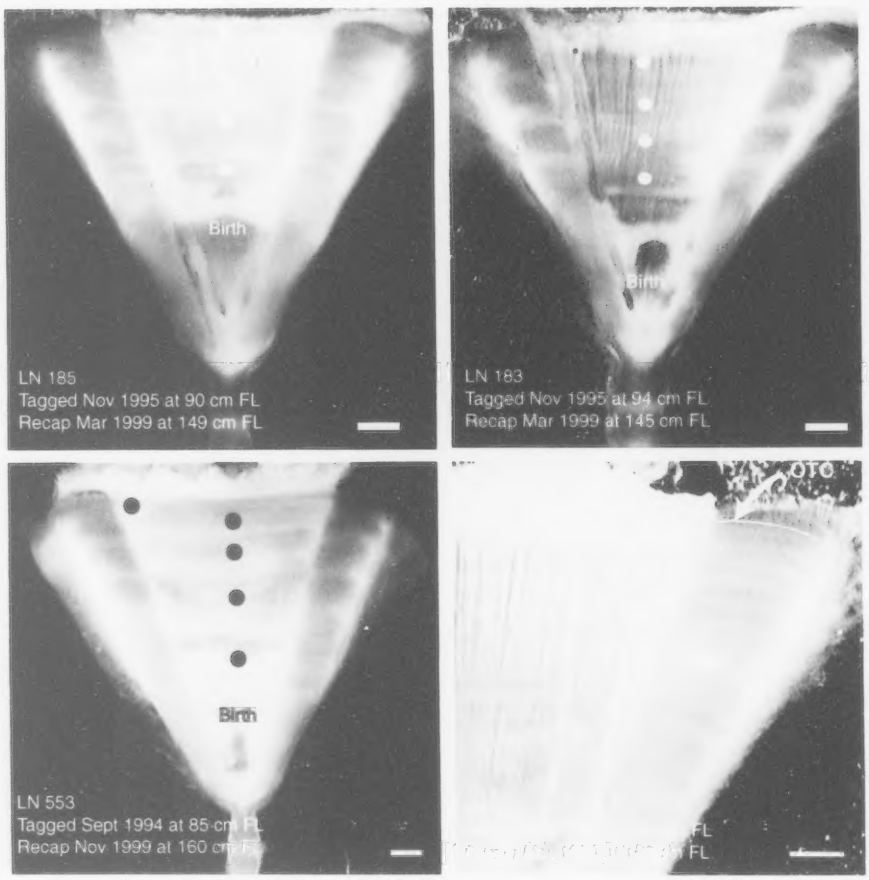
Birth
LN 185
Tagged Nov 1995 at 90 cm FL
Recap Mar 1999 at 149 cm FL
Birth
LN 183
Tagged Nov 1995 at 94 cm FL
Recap Mar 1999 at 145 cm FL
Birth
LN 553
Tagged Sept 1994 at 85 cm FL
Recap Nov 1999 at 160 cm FL
OTC

Figure 3

Vertebral sections from recaptures of three known-age porbeagles and one OTC-injected porbeagle. Annuli are indicated, as is the birth mark. Scale bar = 1 mm.

a mean length of 85 cm FL and grew to a mean length of 98 cm FL by December. Age-1 individuals had a mean length of 106 cm FL in April, 113 cm FL in July, and 123 cm FL in December, resulting in an annual growth of 25 cm/yr between December and December. Although larger length modes were occasionally visible, only the age-0 and age-1 modes were clear and unambiguous throughout the year.

The MULTIFAN models that best fitted the 1991 data were the most complex, having variable standard deviations in length and variable seasonal growth. The data with sexes combined had 18 age classes, whereas males and females had 16 and 15 age classes, respectively. The MULTIFAN L_∞ and K von Bertalanffy parameters fell outside the 95% confidence intervals for the tagging and vertebral studies, although the t_0 values did not (Table 2). These differences are reflected in the VBGF curves as compared with the other methods (Fig. 8). The annual growth rate calculated from the MULTIFAN data was consistent with that of the vertebral and tag-recapture analyses at 150 cm FL (Fig. 6). However, the reliability of the MULTIFAN results is questionable given the large number of age classes in the population. The standard error estimates calculated by MULTIFAN were not reported because they were unrealistically low (Francis and Francis, 1992; Francis and Mulligan, 1998).

Longevity

The maximum ages based on vertebral band pair counts were 25 and 24 years for males and females, respectively. These ages likely underestimate longevity, given the long-

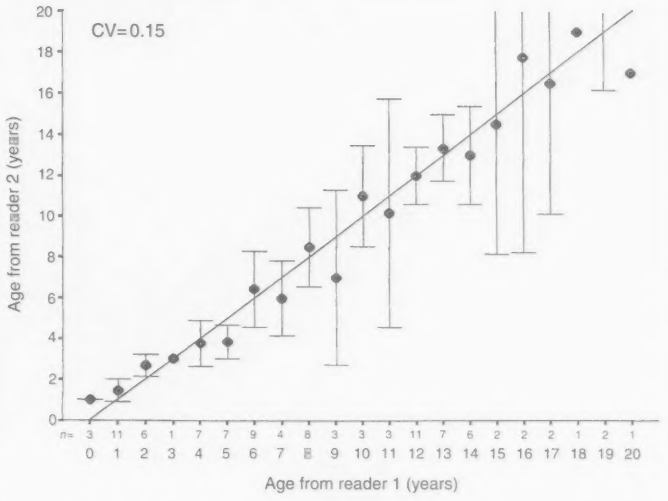

Figure 4

Age bias graph for pair-wise comparison of porbeagle vertebral counts from two independent age readers. Each error bar represents the 95% confidence interval for the mean age assigned by reader 2 to all fish assigned a given age by reader 1. The one to one equivalence line is also presented.

Table 2

Von Bertalanffy growth function parameters and 95% confidence intervals calculated by using vertebral, tag-recapture, and length-frequency methods. Confidence intervals (CI) are not shown for the MULTIFAN parameters. ϕ_1, ϕ_2, are seasonal parameters and t_1 is the time (years) between the theoretical birthday and recruitment to the fishery for the MULTIFAN analyses.

Method		L_∞	K	t_0	n	ϕ_1	ϕ_2	t_1
Vertebral	Combined	289.4	0.066	–6.06	576			
	CI	±16.5	0.010	0.71				
	Male	257.7	0.080	–5.78	283			
	CI	±15.6	0.015	0.92				
	Female	309.8	0.061	–5.90	291			
	CI	±26.2	0.013	0.93				
MULTIFAN	Combined	320.1	0.054	–5.33	13,589	0.95	0.76	0.25
	Male	280.2	0.076	–4.42	7142	0.95	0.92	0.25
	Female	419.0	0.039	–5.45	6269	0.95	0.89	0.25
Gulland and Holt (1959)	Combined	212.5	0.172	–2.21	54			
	CI	±31.7	0.089					
GROTAG	Combined	204	0.194	–2.05	76			

term fishery for this species. Taylor's (1958) method, the age at which 95% of the L_∞ is reached, provided a value of 26 years. However, more realistic estimates of longevity take advantage of estimated mortality rates. Given M=0.10 (Campana et al.[1]), Hoenig's (1983) equation based on multiple species resulted in a longevity estimate of 45 years. The estimate of Campana et al.[2] was species-independent and was calculated by assuming a constant instantaneous rate of mortality = 0.10 in an unfished population. The resulting longevity estimate was 46 years. Each of these methods assumes that M is constant throughout the lifetime of a fish, whereas in fact, it probably increases in sexually mature or senescent fish. Any such increase would result in a lower estimate of longevity. Based on prelim-

Table 3

Log-likelihood function values and parameter estimates for four growth models fitted to porbeagle tagging data by using GROTAG (Francis 1988a). For a significant ($P<0.05$) improvement in fit, the introduction of one extra parameter must increase λ by at least 1.92 (Francis 1988a). * indicates fixed parameters.

Parameter	Symbol (unit)	Model 1	Model 2	Model 3
Log likelihood	λ	–292.04	–291.97	–285.45
Mean growth rates	g_{95} (cm/yr)	19.12	17.92	19.21
	g_{150} (cm/yr)	9.47	8.88	9.52
Measurement error	s (cm)	10.48	10.92	9.43
	m (cm)	0*	0.99	1.00
Outliers	p	0*	0*	0.07

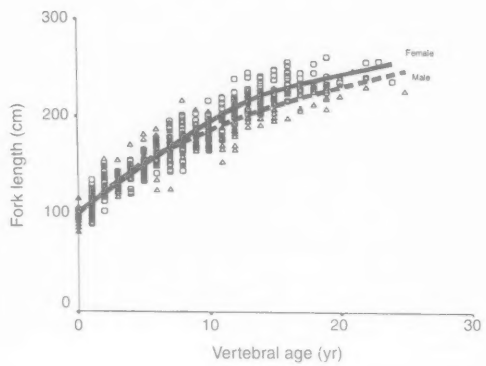

Figure 5

Porbeagle growth data based on vertebral band counts. LOESS curves have been fitted to the data by sex. Open circles represent males, open triangles represent females.

inary results suggesting an increase in female natural mortality rate (to 0.20) at the age of sexual maturity (Campana[6]), longevity would be estimated at 29 years.

Discussion

Age and growth studies of lamnoids have often been confounded because of the continued debate over the periodicity of band-pair formation. Parker and Stott (1965) first suggested that two growth band pairs formed each year (biannual band-pair deposition) in their study of the basking shark (*Cetorhinus maximus*). Pratt and Casey (1983) assumed biannual band-pair deposition for shortfin mako shark, *Isurus oxyrinchus*, based on consistency with length-frequency and tag-recapture analyses. Branstetter and Musick (1994) also suggested biannual band-pair deposition for the sand tiger shark, *Carcharias taurus*, based on marginal increment analysis (MIA) and examination of aquarium-reared sharks. Cailliet et al. (1983, 1985) assumed annual band-pair deposition for Pacific coast shortfin mako and white sharks, *Carcharodon carcharias*, based on marginal increment analysis. Wintner and Cliff (1999) stated that they could not determine band periodicity using marginal increment analysis in the white shark off the coast of South Africa, although one OTC-injected recapture suggested annual deposition. With the exception of Winter and Cliff (1999), direct validation of band periodicity, such as by OTC injection or by known-age tag-recaptures, has not previously been reported in lamnids. Although several studies have attempted validation with MIA (Branstetter and Musick, 1994; Wintner and Cliff, 1999), this technique is not

Table 4

Size at age for the porbeagle (*Lamna nasus*) calculated from von Bertalanffy equations based on tag-recapture, length-frequency, and vertebral data.

	Size (cm, FL)			
			Tag-recapture	
Age (years)	Vertebral	MULTIFAN	Gulland and Holt (1959)	GROTAG
0	95	82	67	67
1	107	94	90	91
2	119	106	109	111
3	130	117	126	127
4	140	128	139	141
5	149	138	151	152
6	158	148	161	161
7	166	157	169	169
8	174	165	176	175
9	181	174	181	180
10	188	181	186	184
11	195	189	190	188
12	201	195	194	191
13	206	202	197	193
14	212	208	199	195
15	217	214	201	197
16	221	220	203	198
17	226	225	205	199
18	230	230	206	200
19	233		207	201
20	237		208	201

[6] Campana, S. 2001. Unpubl. data. Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2

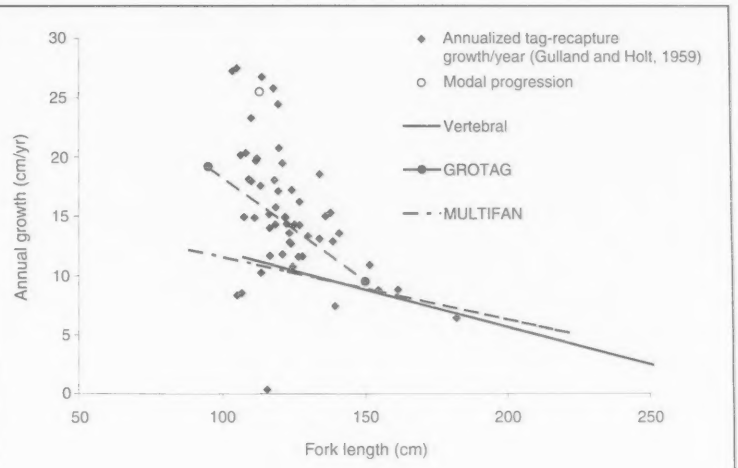

Figure 6

Comparison of the annual growth rate of the porbeagle shark by using multiple aging methods.

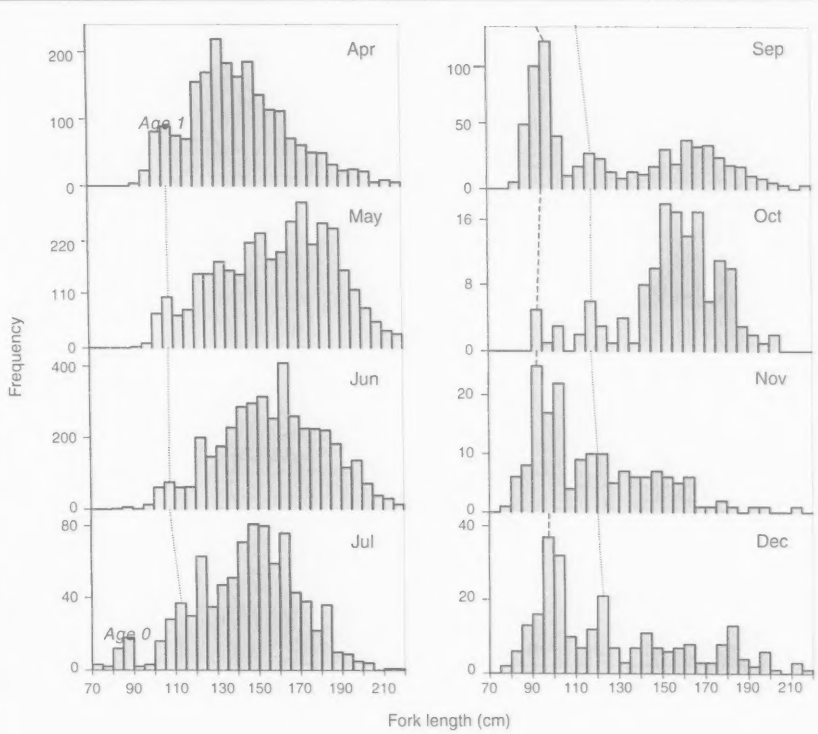

Figure 7

Monthly progressions of age-0 and age-1 length-frequency modes collected by observers in the 1991 Scotian Shelf fishery.

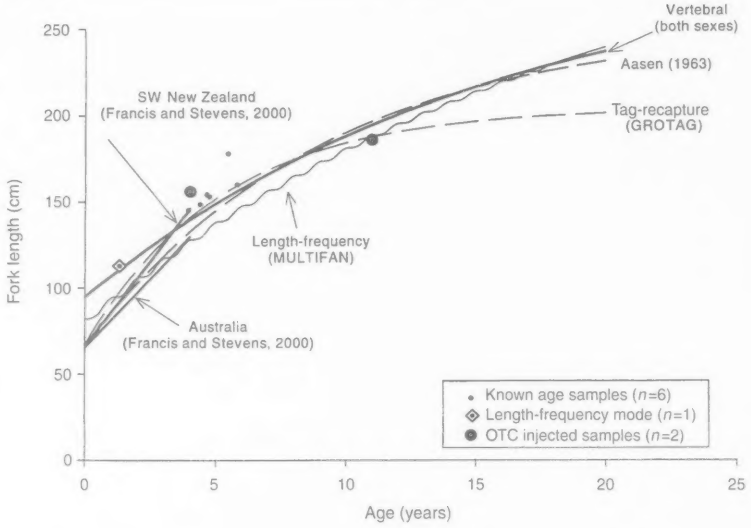

Figure 8

Von Bertalanffy growth curves generated from vertebral data, GROTAG, and MULTIFAN seasonally oscillating parameters, as compared with the length-frequency mode, OTC recaptures, and known-age recaptures (validated). Included for comparison are the von Bertalanffy growth curves of Aasen (1963) and Francis and Stevens (2000).

well suited to slow growing species because the narrowness of the bands at the margin makes it difficult to objectively determine marginal growth.

In the present study, we validated annual band-pair periodicity up to age 11 using recaptures of both OTC-injected and known-age porbeagles. Our data clearly indicated that the vertebral band pairs are deposited annually and that the translucent zone is deposited between November and April.

Validation of an annual frequency of band-pair formation confirms Aasen's (1963) interpretation of the vertebral growth zones in the porbeagle. Our size at birth generated from the vertebral bands (95 cm FL), however, was unrealistically high. This may have been due to our sample of age-0 fish being biased towards the faster growing, larger fish that were recruited first into the fishery. The early portion of our growth curve, corresponding to ages 0 and 1, may therefore have been overestimated (Fig. 8).

Francis (1988b) suggested that growth curves derived from age-length and length-increment data were not directly comparable and that the comparison of growth rates at length was more appropriate. The growth rates at L_{150} were similar for all methods, verifying the growth rate at this size. However, the overall growth curves from the different methods were also similar (Fig. 8). The tag-recapture curve shows a more reasonable early growth than the vertebral curve but levels off well below the observed maximum size. The lower L_∞ and higher K for the tag-recapture method was expected because of the different derivation of the parameters and the absence of recaptured old sharks (Francis, 1988b). The K and t_0 parameters derived from MULTIFAN are close to those obtained by using vertebral ages, and the scatter in the age readings overlaps the MULTIFAN von Bertalanffy curve (Figs. 5 and 8). Although the MULTIFAN L_∞ value was slightly higher than that of the vertebral value (Table 2), a difference at the upper end of these curves was not unexpected because length-frequency models are generally considered unreliable for the older age classes where the modes are not easily defined (Francis and Francis, 1992; Francis, 1997; Francis et al., 1999).

Maturity occurs in the porbeagle at 8 and 13 years of age (174 and 218 cm FL, males and females, respectively; Jensen et al.[4]). Growth for both sexes is similar up to the size of male maturity, whereupon, the male growth rate is reduced. Females continue to grow rapidly until the onset of maturity, at which point their growth slows as well (Fig. 5). Owing to this change in growth rate, males reach a smaller maximum size than females; however, the overall growth rate for both sexes is not substantially different. Additionally, the vertebral L_∞ generated for females is higher than what is being observed in the fishery, suggesting that it has been overestimated and that the combined curve is more appropriate. Aasen[7] (1963) also found no difference in the growth rate between the sexes although the basis for his conclusion is questionable.

[7] Aasen, O. 1961. Some observations on the biology of the porbeagle shark (*Lamna nasus*, L). ICES, C.M. Copenhagen 1961, Near Northern Seas Committee (109):1–7.

Aasen (1963) relied extensively on length-frequency modes to estimate the growth of porbeagle. Although his modes were similar to ours, his interpretation of the age-1 mode differed. Our data indicated that age-0 porbeagle average 85 cm FL in July. Aasen (1963) interpreted this same mode (91 cm FL) as age 1+, thus shifting his ages by one year. Neither Aasen's (1963) modal distribution (his Fig. 4) nor ours, supports the contention that this first mode is age 1+. His classification of these fish as age 1+ was based on size at birth and his opinion that the smallest measured fish were from the age-0 group. There is, however, no mode at this small size. Any age-0 fish born in April and caught between July and September (his sampling period) would certainly be larger than the birth size. Therefore, we feel that these fish represented the faster growing age-0 fish that were large enough to be caught with commercial longline gear. Francis and Stevens (2000) also used length-frequency analysis to estimate the growth rate of porbeagles in the South Pacific. Although their modes were once again comparable to ours, their age 1+ fish were similar in size to our age-0+ fish (Fig. 8). In their view, this first mode represented slow growing age-1 individuals rather than fast growing age-0 individuals. As an alternative explanation, we suggest that the first mode in both the southwest and northeast New Zealand samples represents YOY that have grown during the 4-month sampling period, thus accounting for the apparent absence of individuals close to a birth size. This alternative explanation would also explain why the modal analysis of the Australian sample shows a strong peak at birth and subsequent modes that are similar to ours. If correct, our interpretation of the Francis and Stevens (2000) data would bring their estimates of size at age and growth rate in line with ours. Of course, the comparison of growth rates from such widely separated stocks is difficult, and its value questionable.

Longevity estimates for the porbeagle indicate that they may live for more than 40 years. The maximum time at liberty for any tagged porbeagle is 13 years (Stevens, 1990). The length of this shark when tagged was approximately 120 cm TL (107 cm FL; 1+ years); it was recaptured at an estimated 225 cm FL (age 14+) which would correspond to an age of 16+ years according to our vertebral growth curve. This is substantially less than the oldest observed age from vertebrae (25) and the estimates from the Hoenig (1983) and Campana et al.[2] methods of 45 and 46 years, respectively.

The growth rate and longevity of the porbeagle are similar to those of other lamnids. Wintner and Cliff (1999) calculated a K value of 0.065 for the white shark from the east coast of South Africa, and Cailliet et al. (1985) estimated a K value of 0.058 for the same species off the coast of California. Both estimates are very similar to the K value of 0.066 calculated for porbeagle in our study. Shortfin mako K values have been estimated at 0.072 (Cailliet et al., 1983) and 0.266 (Pratt and Casey, 1983); however the Pratt and Casey value was based on the assumption that two band pairs were deposited annually. Longevity estimates have ranged between 27 years for the California white shark (Cailliet et al., 1985) and 45 years for the shortfin mako in the Pacific (Cailliet et al., 1983).

Comprehensive age and growth studies of pelagic sharks are difficult to implement because many species are highly migratory and are caught sporadically as part of seasonal fisheries. Thus, aging studies of pelagic sharks have usually been less rigorous than desired, despite the oft-repeated call for age validation (Beamish and McFarlane, 1983; Cailliet et al., 1986, Cailliet, 1990). Previous studies on pelagic species such as the blue shark (Stevens, 1975; Cailliet et al., 1983), white shark (Cailliet et al., 1985), thresher (Cailliet et al., 1983), shortfin mako (Cailliet et al, 1983), pelagic thresher (Liu et al., 1999), oceanic whitetip shark (Lessa et al., 1999), and porbeagle (Aasen, 1963; Francis and Stevens, 2000), have included analyses of ages determined by vertebral or length-frequency analyses (or by both methods), but none of the age interpretations were validated. Wintner and Cliff (1999) used vertebral counts and had one OTC-injected recapture but were unable to provide validation or consistency with other methods. Pratt and Casey (1983) aged the shortfin mako by using four methods (temporal analysis of length-month information, tag-recapture data, length-frequency data, and vertebral band counts) but could not validate their age interpretations. The conclusion that band pairs were deposited biannually was based on vertebrae from four tag-recaptures and consistency between methods. Skomal (1986) aged the blue shark in the western North Atlantic using a combination of vertebral, length frequency and tag-recapture methods for verification. Although Skomal (1986) had two OTC-injected recaptures, they provided conflicting results for validation. The present study is the first that has used validated vertebral band-pair counts in conjunction with length-frequency and tag-recapture analyses to provide consistent and accurate age estimates for a pelagic shark species. We suggest that a similar approach would be useful in studies of other pelagic shark species.

Acknowledgments

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Food habits and consumption rates of common dolphinfish (*Coryphaena hippurus*) in the eastern Pacific Ocean

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Abstract–An ecosystem approach to fisheries management requires an understanding of the impact of predatory fishes on the underlying prey resources. Defining trophic connections and measuring rates of food consumption by apex predators lays the groundwork for gaining insight into the role of predators and commercial fisheries in influencing food web structure and ecosystem dynamics. We analyzed the stomach contents of 545 common dolphinfish (*Coryphaena hippurus*) sampled from 74 sets of tuna purse-seine vessels fishing in the eastern Pacific Ocean (EPO) over a 22-month period. Stomach fullness of these dolphinfish and digestion state of the prey indicated that diel feeding periodicity varied by area and may be related to the digestibility and energy content of the prey. Common dolphinfish in the EPO appear to feed at night, as well as during the daytime. We analyzed prey importance by weight, numbers, and frequency of occurrence for five regions of the EPO. Prey importance varied by area. Flyingfishes, epipelagic cephalopods, tetraodontiform fishes, several mesopelagic fishes, *Auxis* spp., and gempylid fishes predominated in the diet. Ratios of prey length to predator length ranged from 0.014 to 0.720. Consumption-rate estimates averaged 5.6% of body weight per day. Stratified by sex, area, and length class, daily rations ranged up to 9.6% for large males and up to 19.8% for small dolphinfish in the east area (0–15°N, 111°W–coastline). Because common dolphinfish exert substantial predation pressure on several important prey groups, we concluded that their feeding ecology provides important clues to the pelagic food web and ecosystem structure in the EPO.

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Dolphinfishes (*Coryphaena hippurus* and *C. equiselis*) are abundant, wide-ranging, epipelagic predators in tropical and subtropical oceans (Palko et al., 1982). They support important commercial, artisanal, and recreational fisheries in several regions (Beardsley, 1967; Oxenford and Hunte, 1986; Patterson and Martinez, 1991; Campos et al., 1993; Norton and Crooke, 1994; Lasso and Zapata, 1999). Dolphinfishes are also a large component of the bycatches of the tuna purse-seine and longline fisheries in the Pacific Ocean (Lawson, 1997; IATTC, 1999). They are commonly found near natural and artificial floating objects (Kojima, 1956; Hunter and Mitchell, 1966; Gooding and Magnuson, 1967; Wickham et al., 1973), a trait which facilitates their capture.

Calls have been issued for developing an ecological approach to fisheries management, taking greater note of species interactions and underlying ecosystem dynamics (FAO, 1995; Larkin, 1996; Mangel et al., 1996; Botsford et al., 1997). Removal of predator biomass by commercial fishing represents a "top-down" disturbance of the system. Selective exploitation of apex predators can have profound effects on pelagic ecosystems because of the removal of predation pressure (Essington et al., in press) and because of top-down, trophic-cascade effects (Shiomoto et al., 1997; Estes et al., 1998; Verheye and Richardson, 1998). An understanding of how top-down processes influence the dynamics of marine communities derives from a basic understanding of the trophic connections and rates of food consumption of the predators. Although four studies have provided limited data on the food habits of dolphinfishes in coastal areas of the eastern Pacific Ocean (EPO) (Hida, 1973; Campos et al., 1993; Aguilar-Palomino et al., 1998; Lasso and Zapata, 1999), little is known of the predation dynamics of dolphinfishes over the majority of their oceanic habitat.

Common dolphinfish (*C. hippurus*) are renowned for their rapid rates of growth and metabolism. In Hawaiian waters, common dolphinfish have attained average lengths of 120 cm and weights of 12.5 kg at 12 months of age (Uchiyama et al., 1986). Standard metabolic rates of common dolphinfish are comparable to those of yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas (Benetti et al., 1995). All three species have large surface areas and thin blood-water interfaces in their gills, morphological features that permit high oxygen diffusion capacity and elevated metabolic rates (Brill, 1996). High energy requirements imply that predators like dolphinfish can account for important amounts of tertiary production removed from an ecosystem (Essington et al., in press), but rates of food consumption by dolphinfish in nature have not been measured.

The objectives of our study were to define the trophic relations of the com-

mon dolphinfish, and their prey in both coastal and oceanic areas of the EPO and to provide preliminary estimates of their daily rates of food consumption.

Materials and methods

The dolphinfish were caught by tuna purse-seine vessels of Colombian, Mexican, Panamanian, and Venezuelan registry from December 1992 through September 1994. The fish were caught as bycatch of the purse-seine fishery for tunas associated with dolphins, with floating objects, and as unassociated schools ("schoolfish"). In dolphin sets, the net is deployed around aggregations of primarily yellowfin tuna and spotted or spinner dolphins (*Stenella attenuata* or *S. longirostris*) (or both dolphin species) after a high-speed chase by speedboats. Floating-object sets are made by encircling flotsam, commonly tree parts and artificial fish-aggregating devices (FADs), and associated fauna with the purse seine, usually in the early morning. Schoolfish are detected by seabird activity and disturbance of the water surface caused by the fish swimming just below. The species composition and size and age distribution of the fauna are distinctly different for the three aggregation types and fishing strategies (Hall, 1998).

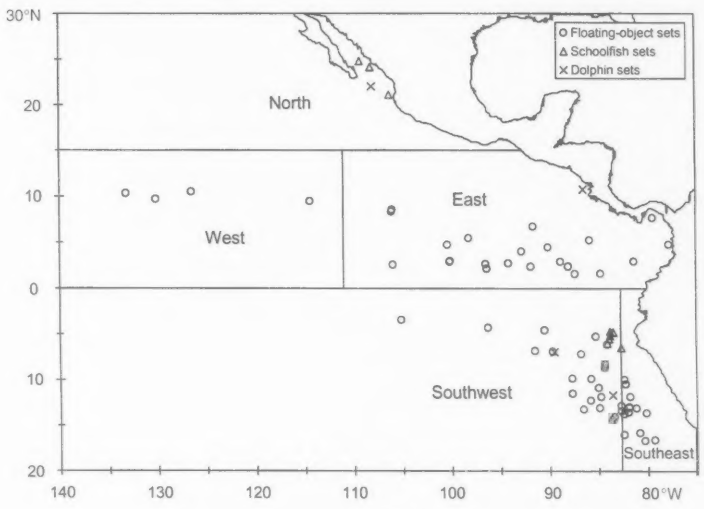

Figure 1

Locations where common dolphinfish samples were caught by three types of purse-seine sets. We stratified the data into the five areas shown.

Stomach samples

Common dolphinfish stomach samples were taken at sea by observers of the Inter-American Tropical Tuna Commission (IATTC). The purse-seine sets yielding the dolphinfish samples were distributed across the geographical range of the EPO tuna fishery at that time (Fig. 1). We obtained samples from 74 purse-seine sets over a 22-month period: 61 sets (82%) were made on floating objects; 4 sets were made on dolphins; and 9 sets were made on unassociated tuna. On board the vessels, the observers measured the fork length (mm) of each dolphinfish, determined the sex if possible, and excised and immediately froze the stomachs. In the laboratory, we thawed the stomachs and visually estimated the stomach fullness as a percentage of the stomach capacity. Then, we identified the stomach contents to the lowest taxon possible, weighed them to the nearest gram, and enumerated them when individuals were recognizable. The counts of paired structures, such as cephalopod mandibles and fish otoliths, were divided by two to estimate numbers of prey. We categorized the digestion state of the prey: 1 = intact or nearly intact; 2 = soft parts partially digested; 3 = whole or nearly whole skeletons without flesh (or comparable state for nonfish taxa); and 4 = only hard parts remaining (primarily fish otoliths and cephalopod mandibles). We measured the length, or maximum dimension of individual prey to the nearest mm, if sufficiently intact. For cephalopods, we recorded the mantle length excluding tentacles.

Identifying the prey depended on the digestion state of the remains. We used the following keys to identify fish prey in digestion state 1: Jordan and Evermann (1896), Meek and Hildebrand (1923), Parin (1961), Miller and Lea (1972), Thomson et al. (1979), Allen and Robertson (1994), and Fischer et al. (1995b and 1995c). When the fishes were digested to state 2 or 3 we used taxonomic keys of vertebral characteristics (e.g. Clothier, 1950; Monod, 1968; Miller and Jorgenson, 1973) and compared skeletons of whole fishes collected in the EPO. We identified the crustacean prey from exoskeleton remains using the keys of Garth and Stephenson (1966), Brusca (1980), and Fischer et al. (1995a). We identified cephalopod prey from mandible remains (Clarke, 1962; Iverson and Pinkas, 1971; Wolff, 1982; Clarke, 1986). The fish collections at Scripps Institution of Oceanography and the Natural History Museum of Los Angeles County, and the cephalopod collection at the Santa Barbara Museum of Natural History were used to compare and validate prey identifications.

Data analysis

We analyzed the diet data by calculating three diet indices for each prey taxon. We calculated gravimetric importance of the prey (%*W*) as percentages of the total prey weights, numerical importance (%*N*) as percentages of total counts, and frequency of occurrence as the number of dolphinfish stomachs that contained a particular prey. We calculated percent occurrence (%*O*) as a percentage of all the dolphinfish sampled, regardless of whether their stomachs contained food. We present these three indices by prey taxon in detailed tables, summarized at several

levels of taxonomic resolution. To facilitate analysis, we also grouped the prey taxa by order (e.g. Tetraodontiformes), family (e.g. Carangidae), genus (e.g. *Auxis* spp.), or functional group (e.g. flyingfishes).

Because the three diet indices provide different insights into predation habits, we applied a graphical representation of these measures, proposed by Cortés (1997), to help interpret the data. We made three-dimensional scatter plots of $\%O$, $\%W$, and $\%N$ for all samples and for the data pooled by sampling area to help evaluate the degree of dominance of particular prey and the feeding strategy (generalized vs. specialized) of the dolphinfish. Although we measured the three components of the index of relative importance (IRI) (Pinkas et al., 1971), we did not calculate IRI values because the index is dependent upon the taxonomic resolution of the prey (Hansson, 1998). Also, for a predator that consumes a large size range of prey (see heading "Prey size," below), the IRI is overly influenced by numerous small prey.

We examined diel feeding characteristics by stratifying the data according to stomach fullness of the predator and digestion state of the prey. The scheme for grouping the data, patterned after Calliet (1976), is diagrammed in Figure 2. Prey in digestion states 1 and 2 were categorized as from "recent" feeding events, whereas prey in states 3 and 4 were categorized as from "previous" feedings. These two strata were further subdivided according to stomach fullness. Prey from stomachs ≤50% full were categorized as "low" fullness or empty, whereas those from stomachs >50% full were categorized as "high" fullness (Fig. 2). We plotted the percent occurrence of the prey items in these four digestion and fullness strata by area and the time of day the sets were made: "early morning" (05:12–09:00), "late morning" (09:01–12:00), "early afternoon" (12:01–15:00), and "late afternoon" (15:01–18:16 hours).

We fitted regression trees (Breiman et al., 1984) to the gravimetric data for each prey group to detect statistically important differences by area and dolphinfish size. Regression trees are well suited for detecting and extracting important relations and complex interactions in multivariate ecological (De'ath and Fabricius, 2000) and fisheries data (Watters and Deriso, 2000). We used a two-step process. For both steps, the $\%W$ of each prey group in the stomach contents was the response variable. For the first step, defining area strata (see next paragraph), we used latitude and longitude as the predictor variables. For the second step, modeling the importance of area and dolphinfish size in explaining variation in the $\%W$ for each prey group, we used area designations (north, west, east, southwest, and southeast) and fork length as the predictor variables. We used the tree functions in S-Plus (MathSoft Inc., 1999) and cross-validation to prune fully grown trees so that only important splits remained. Prediction errors were used as pruning criteria (Breiman et al., 1984; De'ath and Fabricius, 2000).

We stratified the data by area (Fig. 1) according to two criteria. Latitude divisions at 15°N and 0° were based on the spatial and seasonal heterogeneity of the purse-seine sets that provided the samples. All the sets sampled from May through November each year were made north of the equator, and most sets sampled during December through April were made south of the equator. Also, the regression trees indicated that latitude and longitude were important in explaining the variability in the gravimetric data for several prey taxa. Epipelagic-cephalopod taxa were most important in the diet of the common dolphinfish caught east of 82°41′W and south of 1° 46′S, and flyingfishes were most important in the diet of those caught west of 81°W. Therefore, we stratified the data from south of the equator into "southwest" and "southeast" areas separated at 82°41′W (Fig. 1). Similarly, we stratified the data from samples collected between 0° and 15°N into "west" and "east" areas divided at 111°W because a regression tree fitted to the gravimetric data for the Tetraodontiformes indicated that this meridian was important in explaining variation in $\%W$ for this taxon. Tetraodontiformes were more important in the diet of the fish caught west of 111°W.

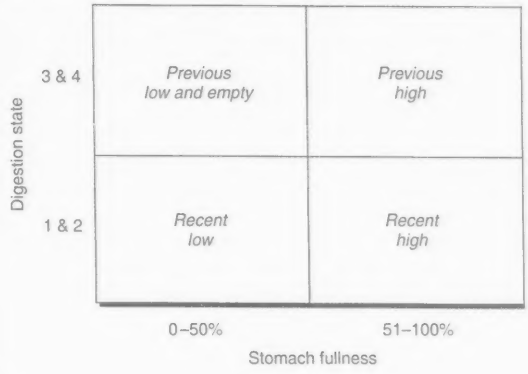

Figure 2

Schematic diagram showing prey digestion-state and predator stomach-fullness criteria for four categories used to analyze diel feeding characteristics of common dolphinfish in the eastern Pacific Ocean.

Consumption rates

We employed a method described by Olson and Mullen (1986) to calculate preliminary estimates of daily rates of food consumption by common dolphinfish. The model predicts feeding rate ($\hat{r}$, grams per hour) by dividing the mean weight of the stomach contents per predator ($\overline{W}$, grams) by the integral (A, proportion × hours=hours) of the function that best fits experimental gastric evacuation data. For a predator that consumes a variety of prey that are evacuated at different rates,

$$\hat{r} = \sum_{i=0}^{I} \frac{\overline{W}_i}{A_i}, \qquad (1)$$

where subscripts i refer to each of I prey types.

Table 1

Numbers of common dolphinfish sampled by size, sex, and area with undigested food in their stomachs (first number) and with empty stomachs or trace amounts of hard parts (in parentheses).

	Sex			Area					
Fork length (mm)	Males	Females	Undetermined sex	North	West	East	Southwest	Southeast	Total no. of dolphinfish
417–650	2 (14)	14 (39)	4 (5)	0 (1)	0 (3)	4 (24)	16 (21)	0 (9)	20 (58)
651–800	12 (21)	48 (47)	8 (3)	1 (0)	2 (9)	14 (11)	37 (47)	14 (4)	68 (71)
801–950	24 (29)	51 (70)	11 (7)		11 (11)	13 (13)	43 (60)	19 (22)	86 (106)
951–1100	26 (25)	15 (21)	3 (1)		0 (2)	10 (10)	19 (19)	15 (16)	44 (47)
1101–1250	9 (6)	10 (6)	2 (1)	2 (0)		10 (5)	5 (1)	4 (7)	21 (13)
1251–1770	6 (1)	1 (1)	0 (1)			1 (1)	2 (1)	4 (1)	7 (3)
Total	79 (96)	139 (184)	29 (18[1])	3 (1)	13 (25)	52 (64)	122 (150[1])	56 (59)	246 (299[1])

[1] Including one dolphinfish with no length or sex data.

Daily meal is $\hat{r}$ multiplied by 24 h for fish that feed both day and night. Daily ration is daily meal expressed as a percent of body weight. We estimated the body weight of each dolphinfish from the length, according to the relationships of Lasso and Zapata (1999):

$$M = aL^b, \quad (2)$$

where M = body weight (g); and
L = fork length (cm).

They estimated that $a = 0.0406$, 0.0420, and 0.0224, and $b = 2.6588$, 2.6328, and 2.78 for males, females, and common dolphinfish of undetermined sex, respectively. We estimated daily consumption rates for dolphinfish of six size strata by sex and area.

The time-course of gastric evacuation has not been adequately described for dolphinfishes. This fact prevents a rigorous analysis of consumption rates using stomach-contents data. However, we provide preliminary, first-order estimates of daily rations of common dolphinfish because this information is important for analyses of ecosystem effects of fishing (see "Discussion" section). A preliminary experiment indicated that the gastric evacuation rate for squid tissue by juvenile dolphinfish is comparable to that for squid by yellowfin tuna. Five juvenile common dolphinfish passed pellets of moist squid tissue through the digestive tract in 6–8 h at 27°C (Suzuki, 1992). The fastest gastric evacuation times for squid (*Loligo opalescens*) voluntarily ingested by yellowfin tuna (mean L=36.2 cm) in the laboratory were about 8 h at 23.5–25.5°C (Olson and Boggs, 1986). We assume, therefore, that gastric evacuation rates measured for yellowfin tuna are adequate for estimating daily rations of dolphinfish. We assigned values of A (Eq. 1) for squid (4.48), mackerel (*Scomber japonicus*) (5.29), smelt (*Hypomesus pretiosus*) (4.12), and nehu (*Stolephorus purpureus*) (2.24), and the mean for four experimental food species (3.77) determined by Olson and Boggs (1986) to the various prey taxa of common dolphinfish, as they did for yellowfin tuna. We omitted the data for the trace hard parts (cephalopod mandibles and fish otoliths), which apparently accumulate in the stomachs, when calculating consumption rates because of the possibility that these remained from predation on previous days.

Results

Stomach samples were obtained from 545 dolphinfish: 175 males, 323 females, and 47 of undetermined sex. Two hundred and forty-six specimens had fresh or partially digested food remains in their stomachs, 274 had empty stomachs, and 25 had only trace amounts of digestion-resistant hard parts (cephalopod mandibles and fish otoliths). We present the sample sizes by sex and area in Table 1 and the detailed prey-composition data by area in Tables 2–4. We analyzed the prey composition data by sex but did not discover important differences or trends.

Few samples were obtained in the north and west areas. Therefore, we briefly summarize those data here and in Tables 2–4 and do not include them in the detailed treatments of diel feeding periodicity, diet measures by area, and size-specific predation. Only four common dolphinfish were sampled in the north area, three from sets on schoolfish and one from a set on dolphins. Three of the stomach samples contained food and one was empty. A large dolphinfish (1149 mm) had recently eaten a large squid (*Sthenoteuthis oualaniensis*) in the early morning. Another large fish (1239 mm) had a full stomach containing 7 fresh *Coryphaena equiselis* in the late afternoon. Both fish had been collected from schoolfish sets. A smaller dolphinfish (768 mm) from a dolphin set in the late afternoon had remains of various taxa, principally *C. equiselis*, flyingfishes, and galatheid red crabs (*Pleuroncodes planipes*) in advanced states of digestion. In addition, a 564-mm dolphinfish from a schoolfish set was found to have an empty stomach.

Thirty-eight common dolphinfish were sampled in the west area from 4 sets on floating objects between 05:40 and

Table 2

Taxonomic composition in %*W* of the prey of common dolphinfish from five areas of the eastern Pacific Ocean (Fig. 1) and from all areas combined. Weights do not include hard parts (cephalopod mandibles and fish otoliths). Prey category codes are as follows: EC = epipelagic cephalopods, MC = mesopelagic cephalopods, Cr = Crustacea, MiF = miscellaneous fishes, MsF = mesopelagic fishes, F = flyingfishes, Co = Coryphaenidae, Ca = Carangidae, G = Gempylidae, A = *Auxis* spp., YT = yellowfin tuna, N = Nomeidae, T = Tetraodontiformes. A_i is the integral of the function fitted to experimental gastric evacuation data and is used to calculate consumption rates (Eq. 1). Area codes are N = north, W = west, E = east, SW = southwest, SE = southeast.

Taxon	Category	Assumed A_i	Area					
			N	W	E	SW	SE	All
Phylum Mollusca		4.48	16.35	2.54	9.48	21.69	82.73	32.20
Class Cephalopoda		4.48	16.35	2.54	9.48	21.69	82.73	32.19
Order Teuthoidea		4.48	16.35	2.54	9.48	21.66	81.84	31.91
Family Enoploteuthidae	EC	4.48		*		*	*	*
Abraliopsis falco	EC	4.48		*		*	*	*
Family Mastigoteuthidae	MC	4.48			0.15	0.01		0.04
Mastigoteuthis spp.	MC	4.48			0.15	0.01		0.04
Family Ommastrephidae	EC	4.48	16.35	2.54	5.47	21.40	81.84	30.72
Dosidicus gigas	EC	4.48		2.54	0.78	5.08	70.73	19.27
Sthenoteuthis oualaniensis	EC	4.48	16.35		4.69	16.32	11.11	11.45
Family Onychoteuthidae	EC	4.48			3.26	0.09		0.91
Onychoteuthis banksii	EC	4.48			3.26	0.09		0.91
Onychoteuthis spp.	EC	4.48				*		*
Family Pholidoteuthidae	EC	4.48				*		*
Pholidoteuthis boschmani	EC	4.48				*		*
Family Thysanoteuthidae	EC	4.48			*	0.17		0.07
Thysanoteuthis rhombus	EC	4.48			*	0.17		0.07
Order Octopoda	EC	4.48		*	*	0.02	1.16	0.29
Family Tremoctopodidae	EC	4.48					1.16	0.28
Tremoctopus violaceus	EC	4.48					1.16	0.28
Family Argonautidae	EC	4.48		*	*	0.02	*	0.01
Argonauta spp.	EC	4.48		*	*	0.02	*	0.01
Family Bolitaenidae	MC	4.48		*		*		*
Japetella diaphana	MC	4.48		*		*		*
Phylum Arthropoda		3.37	1.39		3.26	0.01		0.94
Class Crustacea	Cr	3.37	1.39		3.26	0.01		0.94
Order Decapoda	Cr	3.37	1.39		3.26	0.01		0.94
Family Galatheidae	Cr	3.37	1.39					0.06
Pleuroncodes planipes	Cr	3.37	1.39					0.06
Family Penaeidae	Cr	3.37			0.61			0.16
Family Portunidae	Cr	3.37			2.65			0.71
Portunus xantusii	Cr	3.37			2.65			0.71
Phylum Chordata		4.12	82.26	97.46	87.24	78.30	17.00	66.84
Class Osteichthyes		4.12	82.26	97.46	87.24	78.30	17.00	66.84
Order Clupeiformes	MiF	4.12			0.08			0.02
Family Engraulidae	MiF	4.12			0.08			0.02
Order Stomiiformes	MsF	2.24			0.48	4.53		2.01
Family Phosichthyidae	MsF	2.24			0.48	4.53		2.01
Vinciguerria lucetia	MsF	2.24			0.48	4.53		2.01
Order Myctophiformes	MsF	2.24	0.07	4.26	3.11	*		0.97
Family Myctophidae	MsF	2.24	0.07	4.26	3.11	*		0.97
Benthosema panamense	MsF	2.24		*				*

continued

Table 2 (continued)

Taxon	Category	Assumed A_i	Area					
			N	W	E	SW	SE	All
Myctophum aurolaternatum	MsF	2.24			0.97			0.26
Myctophum nitidulum	MsF	2.24			*			*
Symbolophorus spp.	MsF	2.24		4.26	2.14	*		0.71
Order Lampridiformes	MsF	5.29				3.04		1.27
Family Trachipteridae	MsF	5.29				3.04		1.27
Desmodesma polystictum	MsF	5.29				3.04		1.27
Order Beloniformes			1.59	26.50	49.58	31.64	9.29	29.58
Family Belonidae	MiF	5.29			0.26		1.34	0.39
Strongylura spp.	MiF	5.29			0.26		1.34	0.39
Family Exocoetidae	F	4.12		16.14	30.77	28.43	7.95	22.48
Cheilopogon furcatus	F	4.12				0.66		0.27
Cheilopogon spilonotopterus	F	4.12				0.12		0.05
Cheilopogon spp.	F	4.12		10.96	0.53	3.59	2.94	2.68
Exocoetus monocirrhus	F	4.12			19.19	0.69	1.09	5.69
Exocoetus volitans	F	4.12		5.18	5.34	17.64	1.58	9.31
Exocoetus spp.	F	4.12			0.92	5.04	1.81	2.77
Hirundichthys speculiger	F	4.12			3.17		0.53	0.98
Prognichthys spp.	F	4.12			1.22	0.47		0.52
Family Hemiramphidae	F	4.12	1.59	10.36	18.55	3.21		6.71
Oxyporhamphus micropterus	F	4.12	1.59	10.36	18.55	3.21		6.71
Order Perciformes			80.11		32.60	36.32	5.76	28.90
Family Echeneidae	MiF	3.77				2.48		1.03
Rhombochirus osteochir	MiF	3.77				2.48		1.03
Family Coryphaenidae	Co	5.29	80.11		1.43	2.36	0.20	5.08
Coryphaena equiselis	Co	5.29	80.11			0.01		3.67
Coryphaena hippurus	Co	5.29				1.23		0.51
Family Carangidae	Ca	5.29			0.34	5.48		2.37
Naucrates ductor	Ca	5.29			0.34	3.88		1.71
Family Gempylidae	G	5.29			16.53	3.93	0.01	6.07
Gempylus serpens	G	5.29			16.53	3.93	0.01	6.07
Family Scombridae	MiF	5.29			13.18	15.97	5.54	11.50
Acanthocybium solandri	MiF	5.29			0.04			0.01
Auxis spp.	A	5.29			10.15	15.78		9.29
Euthynnus lineatus	MiF	5.29			1.50			0.40
Thunnus spp.	YT	5.29			1.49	0.19	5.54	1.80
Family Nomeidae	N	2.24			1.12	6.11		2.84
Cubiceps pauciradiatus	N	2.24			1.12	6.11		2.84
Order Tetraodontiformes	T	3.77	0.49	66.70	1.38	2.77		3.63
Family Balistidae	T	3.77	0.21	38.78				1.22
Xantichthys mento	T	3.77		38.78				1.21
Family Ostraciidae	T	3.77		25.99				0.81
Lactoria diaphanum	T	3.77		25.99				0.81
Family Tetraodontidae	T	3.77	0.28	1.93	1.38	2.77		1.60
Lagocephalus lagocephalus	T	3.77	0.28	1.93	1.38	2.77		1.60
Unidentified fishes	MiF	3.77					1.95	0.47
Total prey weight (g)			1443	985	8459	13,118	7523	31,527

* Only trace quantities of hard parts were present.

Table 3

Taxonomic composition in *%N* of the prey of common dolphinfish from five areas of the eastern Pacific Ocean (Fig. 1) and from all areas combined. Numbers include hard parts (cephalopod mandibles and fish otoliths) divided by two. Numbers are not complete for some taxa because sometimes prey could not be enumerated due to being in an advanced digestion state. Area codes are N = north, W = west, E = east, SW = southwest, SE = southeast.

	Area					
Taxon	N	W	E	SW	SE	All
Phylum Mollusca	2.17	12.36	24.46	19.97	87.35	37.43
Class Cephalopoda	2.17	12.36	24.46	19.97	87.35	37.37
Order Teuthoidea	2.17	7.87	24.21	16.93	85.25	35.27
Family Enoploteuthidae		1.12		3.62	0.23	1.62
Abraliopsis falco		1.12		3.62	0.23	1.62
Family Mastigoteuthidae			0.24	0.29		0.18
Mastigoteuthis spp.			0.24	0.29		0.18
Family Ommastrephidae	2.17	6.74	4.60	11.87	85.01	28.20
Dosidicus gigas		6.74	2.91	9.99	82.20	26.23
Sthenoteuthis oualaniensis	2.17		1.69	1.74	2.81	1.92
Family Onychoteuthidae			18.16	0.72		4.79
Onychoteuthis banksii			18.16	0.58		4.73
Onychoteuthis spp.				0.14		0.06
Family Pholidoteuthidae				0.29		0.12
Pholidoteuthis boschmani				0.29		0.12
Family Thysanoteuthidae			0.24	0.14		0.12
Thysanoteuthis rhombus			0.24	0.14		0.12
Order Octopoda		4.49	0.24	3.04	2.11	2.10
Family Tremoctopodidae					0.94	0.24
Tremoctopus violaceus					0.94	0.24
Family Argonautidae		2.25	0.24	2.75	1.17	1.62
Argonauta spp.		2.25	0.24	2.75	1.17	1.62
Family Bolitaenidae		2.25		0.29		0.24
Japetella diaphana		2.25		0.29		0.24
Phylum Arthropoda	69.57		12.38	0.14		5.05
Class Crustacea	69.57		12.38	0.14		5.05
Order Decapoda	69.57		12.38	0.14		5.03
Family Galatheidae	69.57					1.92
Pleuroncodes planipes	69.57					1.92
Family Penaeidae			1.69			0.42
Family Portunidae			10.65			2.63
Portunus xantusii			10.65			2.63
Phylum Chordata	2.17	87.64	62.95	79.88	12.65	57.31
Class Osteichthyes	2.17	87.64	62.95	79.88	12.65	57.31
Order Clupeiformes			0.48			0.12
Family Engraulidae			0.48			0.12
Order Stomiiformes			*	41.97		17.37
Family Phosichthyidae			*	41.97		17.37
Vinciguerria lucetia			*	41.97		17.37
Order Myctophiformes	2.17	57.30	14.77	0.14		6.83
Family Myctophidae	2.17	57.30	14.77	0.14		6.83
Benthosema panamense		16.85				0.90

continued

Table 3 (continued)

Taxon	Area					
	N	W	E	SW	SE	All
Myctophum aurolaternatum			3.39			0.84
Myctophum nitidulum			3.15			0.78
Symbolophorus spp.		40.45	8.23	0.14		4.25
Order Lampridiformes				0.58		0.24
Family Trachipteridae				0.58		0.24
Desmodesma polystictum				0.58		0.24
Order Beloniformes	4.35	11.24	36.08	29.52	10.77	24.61
Family Belonidae			0.24		0.23	0.12
Strongylura spp.			0.24		0.23	0.12
Family Exocoetidae		6.74	19.13	26.34	10.54	18.68
Cheilopogon furcatus				0.29		0.12
Cheilopogon spilonotopterus				0.29		0.12
Cheilopogon spp.		2.25	0.48	1.74	2.34	1.56
Exocoetus monocirrhus			8.96	0.87	0.47	2.69
Exocoetus volitans		4.49	5.33	13.31	3.51	7.96
Exocoetus spp.			1.94	9.55	3.98	5.45
Hirundichthys speculiger			1.45		0.23	0.42
Prognichthys spp.			0.97	0.29		0.36
Family Hemiramphidae	4.35	4.49	16.71	3.18		5.81
Oxyporhamphus micropterus	4.35	4.49	16.71	3.18		5.81
Order Perciformes	17.39		10.41	6.80	1.64	6.29
Family Echeneidae				0.29		0.12
Rhombochirus osteochir				0.29		0.12
Family Coryphaenidae	17.39		0.24	0.72	0.47	0.96
Coryphaena equiselis	17.39			0.14		0.54
Coryphaena hippurus				0.29		0.12
Family Carangidae			0.97	1.88		1.02
Naucrates ductor			0.97	1.45		0.84
Family Gempylidae			3.63	1.01	0.47	1.44
Gempylus serpens			3.63	1.01	0.47	1.44
Family Scombridae			1.69	1.88	0.70	1.38
Acanthocybium solandri			0.24			0.06
Auxis spp.			0.97	1.74		0.96
Euthynnus lineatus			0.24			0.06
Thunnus spp.			0.24	0.14	0.70	0.30
Family Nomeidae			3.87	1.01		1.38
Cubiceps pauciradiatus			3.87	1.01		1.38
Order Tetraodontiformes	4.35	19.10	1.21	0.72		1.74
Family Balistidae	2.17	2.25				0.18
Xantichthys mento		2.25				0.12
Family Ostraciidae		15.73				0.84
Lactoria diaphanum		15.73				0.84
Family Tetraodontidae	2.17	1.12	1.21	0.72		0.72
Lagocephalus lagocephalus	2.17	1.12	1.21	0.72		0.72
Unidentified fishes				0.14	0.23	0.12
Total number of prey	46	89	412	691	427	1665

* Individual prey could not be enumerated.

Table 4

Taxonomic composition in *%O* of the prey of common dolphinfish from five areas of the eastern Pacific Ocean (Fig. 1) and from all areas combined. The occurrence of hard parts (cephalopod mandibles and fish otoliths) was included. Area codes are N = north, W = west, E = east, SW = southwest, SE = southeast.

	Area					
Taxon	N	W	E	SW	SE	All
Phylum Mollusca	25.0	15.79	15.52	14.34	45.22	21.28
Class Cephalopoda	25.0	15.79	15.52	13.97	45.22	21.10
Order Teuthoidea	25.0	10.53	15.52	12.13	43.48	19.45
Family Enoploteuthidae		2.63		0.37	0.87	0.55
Abraliopsis falco		2.63		0.37	0.87	0.55
Family Mastigoteuthidae			0.86	0.74		0.55
Mastigoteuthis spp.			0.86	0.74		0.55
Family Ommastrephidae	25.0	7.89	8.62	10.29	43.48	16.88
Dosidicus gigas		7.89	6.03	7.35	37.39	13.39
Sthenoteuthis oualaniensis	25.0		4.31	2.57	8.70	4.22
Family Onychoteuthidae			9.48	1.84		2.94
Onychoteuthis banksii			9.48	1.47		2.75
Onychoteuthis spp.				0.37		0.18
Family Pholidoteuthidae				0.74		0.37
Pholidoteuthis boschmani				0.74		0.37
Family Thysanoteuthidae			0.86	0.37		0.37
Thysanoteuthis rhombus			0.86	0.37		0.37
Order Octopoda		7.89	0.86	3.68	5.22	3.67
Family Tremoctopodidae					3.48	0.73
Tremoctopus violaceus					3.48	0.73
Family Argonautidae		5.26	0.86	3.68	1.74	2.75
Argonauta spp.		5.26	0.86	3.68	1.74	2.75
Family Bolitaenidae		2.63		0.74		0.55
Japetella diaphana		2.63		0.74		0.55
Phylum Arthropoda	25.0		8.62	1.10		2.75
Class Crustacea	25.0		8.62	1.10		2.75
Order Decapoda	25.0		7.76	0.37		2.02
Family Galatheidae	25.0					0.18
Pleuroncodes planipes	25.0					0.18
Family Penaeidae			4.31			0.92
Family Portunidae			3.45			0.73
Portunus xantusii			3.45			0.73
Phylum Chordata	50.0	36.84	43.10	42.28	25.22	38.53
Class Osteichthyes	50.0	36.84	43.10	42.28	25.22	38.53
Order Clupeiformes			0.86			0.18
Family Engraulidae			0.86			0.18
Order Stomiiformes			0.86	2.21		1.28
Family Phosichthyidae			0.86	2.21		1.28
Vinciguerria lucetia			0.86	2.21		1.28
Order Myctophiformes	25.0	10.53	6.90	0.37		2.57
Family Myctophidae	25.0	10.53	6.90	0.37		2.57
Benthosema panamense		2.63				0.18

continued

Table 4 (continued)

Taxon	Area					
	N	W	E	SW	SE	All
Myctophum aurolaternatum			6.03			1.28
Myctophum nitidulum			0.86			0.18
Symbolophorus spp.		7.89	3.45	0.37		1.47
Order Lampridiformes				0.74		0.37
Family Trachipteridae				0.74		0.37
Desmodesma polystictum				0.74		0.37
Order Beloniformes	25.0	13.16	36.21	32.35	20.00	29.17
Family Belonidae			0.86		0.87	0.37
Strongylura spp.			0.86		0.87	0.37
Family Exocoetidae		13.16	25.86	28.68	19.13	24.77
Cheilopogon furcatus				0.74		0.37
Cheilopogon spilonotopterus				0.37		0.18
Cheilopogon spp.		5.26	1.72	4.04	4.35	3.67
Exocoetus monocirrhus			12.07	0.74	0.87	3.12
Exocoetus volitans		7.89	6.90	18.01	6.09	12.29
Exocoetus spp.			2.59	6.99	9.57	6.06
Hirundichthys speculiger			1.72		0.87	0.55
Prognichthys spp.			1.72	0.74		0.73
Family Hemiramphidae	25.0	2.63	24.14	6.99		8.99
Oxyporhamphus micropterus	25.0	2.63	24.14	6.99		8.99
Order Perciformes	50.0		17.24	11.40	5.22	10.83
Family Echeneidae				0.37		0.18
Rhombochirus osteochir				0.37		0.18
Family Coryphaenidae	50.0		0.86	1.84	1.74	1.83
Coryphaena equiselis	50.0			0.37		0.55
Coryphaena hippurus				0.74		0.37
Family Carangidae			1.72	1.84		1.28
Naucrates ductor			1.72	1.47		1.10
Family Gempylidae			7.76	1.47	0.87	2.57
Gempylus serpens			7.76	1.47	0.87	2.57
Family Scombridae			5.17	4.41	2.61	3.85
Acanthocybium solandri			0.86			0.18
Auxis spp.			2.59	4.04		2.57
Euthynnus lineatus			0.86			0.18
Thunnus spp.			0.86	0.37	2.61	0.92
Family Nomeidae			6.90	1.84		2.39
Cubiceps pauciradiatus			6.90	1.84		2.39
Order Tetraodontiformes	25.0	18.42	3.45	1.47		2.94
Family Balistidae	25.0	5.26				0.55
Xantichthys mento		5.26				0.37
Family Ostraciidae		10.53				0.73
Lactoria diaphanum		10.53				0.73
Family Tetraodontidae	25.0	2.63	3.45	1.47		1.83
Lagocephalus lagocephalus	25.0	2.63	3.45	1.47		1.83
Unidentified fishes				0.74	0.87	1.10
Total number of samples	4	38	116	272	115	545

08:34 hours; 13 fish had stomachs with undigested food remains, 23 had stomachs that were empty, and 2 had stomachs that contained only trace amounts of hard parts. One of the two dolphinfish in the 651–800 mm size group contained remains of flyingfishes and the other contained tetraodontid puffers. In the larger group (801–950 mm), 11 dolphinfish ate mostly triggerfishes (Balistidae), boxfish (Ostraciidae), and flyingfishes. In addition, 3 fish ≤650 mm and 2 fish in the 951–1100 mm class had empty stomachs or contained only trace amounts of hard parts.

Diel feeding periodicity

Although common dolphinfish are thought to be visual predators that feed primarily in the daytime (Massutí et al., 1998), our data suggest that they also feed at night. In the areas where sufficient sample sizes were obtained (east, southwest, and southeast), an average of about 15% of the dolphinfish caught in the early morning contained food classified in the "previous-high" category (Fig. 3). Many of these prey were flyingfishes, cephalopods, dolphinfishes, wahoo, and snake mackerel in digestion states 3 or 4 and were found in stomachs that were over 50% full. Prey of these or similar taxa were found to be completely evacuated from the stomachs of yellowfin tuna in about 6–18 h (Olson and Boggs, 1986). If dolphinfish gastric evacuation rates are on the order of those of yellowfin tuna (see "Discussion," and "Consumption rates" sections), these prey would have been ingested during the night.

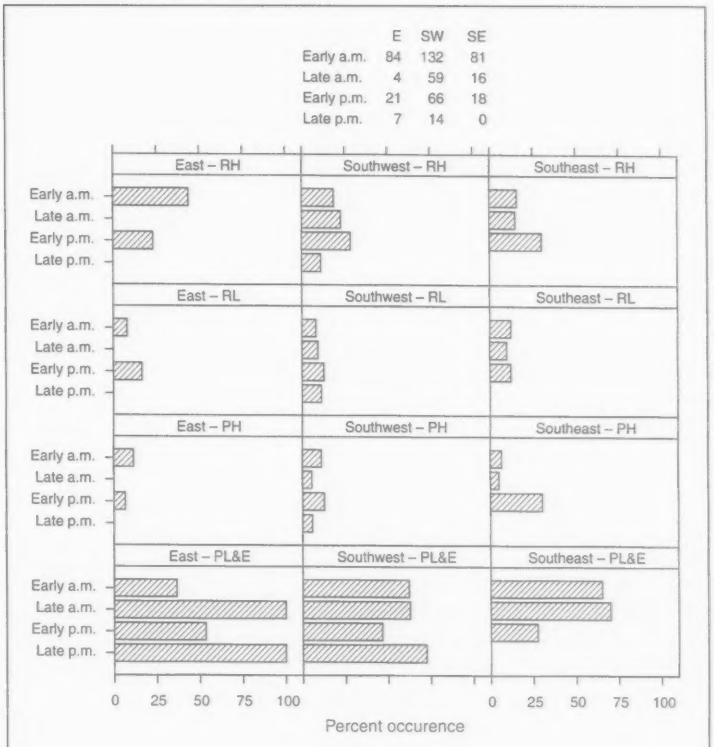

Figure 3

Percent occurrence of the prey items of common dolphinfish corresponding to four fullness-digestion categories (defined in Fig. 2) in three areas of the eastern Pacific Ocean (Fig. 1) and by the time of day the sets were made. RH = recent high, RL = recent low, PH = previous high, PL&E = previous low and empty. Early a.m. = 05:12–09:00, Late a.m. = 09:01–12:00, Early p.m. = 12:01–15:00, Late p.m. = 15:01–18:16 hours. Sample sizes for each time-area stratum are shown at the top. Data for the north area are not shown because the sample size was too small, nor for the west area because only one time stratum was represented.

We examined the time of day that the dolphinfish fed, by area. In the east area, the data indicated peak feeding activity in the early morning and early afternoon, although few samples were obtained in the late morning and late afternoon (Fig. 3, "recent high"). The most important prey taxa by percent biomass in the early morning were flyingfishes (54%), snake mackerel (Gempylidae, 18%), and epipelagic cephalopods (10%). The most important prey taxa in the early afternoon were frigate or bullet tunas (*Auxis* spp., 37%) (or a combination of both), pelagic portunid crabs (27%), and *Thunnus* spp. (yellowfin and bigeye tunas, 15%).

In the southwest area, feeding appears to have occurred throughout the day (Fig. 3). The frequency of observations in the two "recent" categories combined was highest in the early afternoon (41%) and lowest in the late afternoon (22%). The highest proportion of empty stomachs and those containing only residual hard parts occurred in the late afternoon, followed by the early and late morning. The flyingfishes dominated in the diet between 09:00 and 15:00 hours (64% and 57% by weight), and 71% of the diet of dolphinfish caught in the late afternoon was epipelagic cephalopods. The important prey in the early morning were more varied and comprised frigate and bullet tunas (*Auxis* spp., 28%), flyingfishes (18%), epipelagic cephalopods (17%), and mesopelagic fishes (primarily *Vinciguerria lucetia*, 15%).

In the southeast area, although no samples were obtained in the late afternoon, the data suggested peak feeding activity in the early afternoon (Fig. 3). The frequency of observations in both "recent" categories in the early afternoon summed to 42% of the total, compared with only 25% in the late morning. Most of the empty stomachs were from fish captured in sets made before noon. The epipelagic cephalopod *Dosidicus gigas* dominated in the diet during all time periods. Fifteen percent of the stomach contents of the common dolphinfish caught before 09:00 hours were small yellowfin tuna.

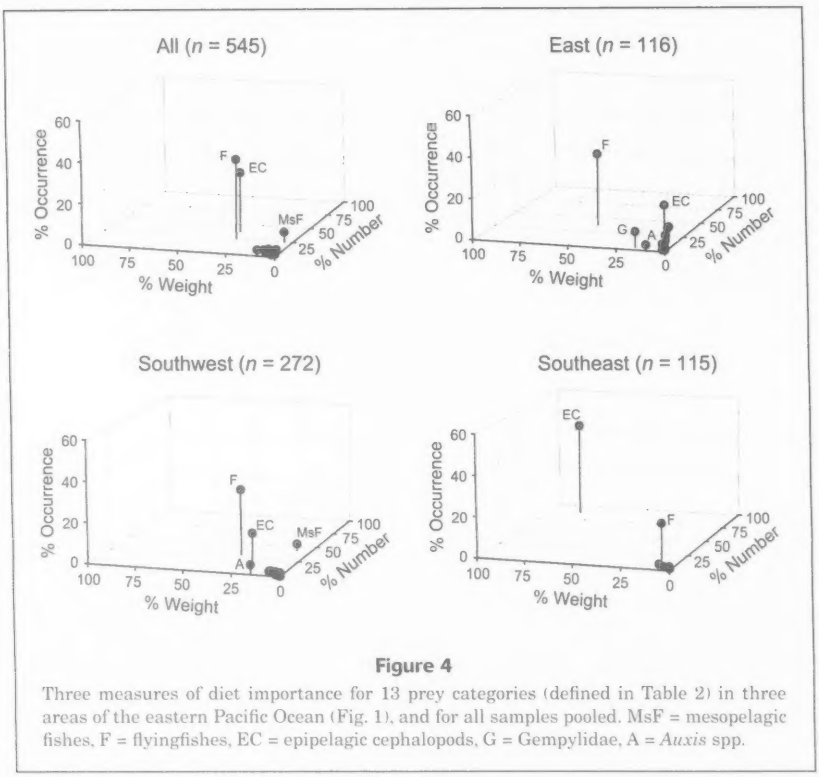

Figure 4

Three measures of diet importance for 13 prey categories (defined in Table 2) in three areas of the eastern Pacific Ocean (Fig. 1), and for all samples pooled. MsF = mesopelagic fishes, F = flyingfishes, EC = epipelagic cephalopods, G = Gempylidae, A = *Auxis* spp.

Diet measures by area

We present three measures of diet importance, $\%W$, $\%N$, and $\%O$, in Figure 4 for all samples pooled, and by area. We included the data for trace quantities of hard parts (cephalopod mandibles and fish otoliths) in the analysis of $\%N$ and $\%O$, but not of $\%W$.

The graphical representation indicates that, when all data are pooled, most components of the diet appear to be quite rare (close to the origin of the graph, Fig. 4, all). However, when the data are examined by area, the diet proves to be more varied. Flyingfishes and epipelagic cephalopods were clearly the dominant prey. Overall, flyingfishes were eaten by more of the dolphinfish (29% occurrence) than any other category, followed by epipelagic cephalopods (21% occurrence). Because 274 stomach samples were totally empty, these are equivalent to 58% and 42% occurrence, respectively, in the stomachs that contained food or hard parts. Prey counts contributed more than prey biomass to the apparent importance of mesopelagic fishes and epipelagic cephalopods in the diet. This is partly due to the accumulation of digestion-resistant hard parts of these two taxa in the stomachs.

Area was an important source of variation in the $\%W$ of three prey groups. The regression tree for epipelagic cephalopods indicated that 25% of the apparent variation in the $\%W$ of that prey was explained by area (southeast vs. others). Area was also an important predictor of flyingfish predation; 15% of the apparent variation in the $\%W$ was explained by area (north, west, and southeast vs. other areas). The regression tree for Tetraodontiformes indicated that 41% of the apparent variation in predation on that taxon was explained by area (west *vs.* others). The gravimetric importance of the 10 other prey taxa could not be modeled by regression trees (i.e. the trees pruned back to the overall mean $\%W$ for those prey) owing to their infrequency in the diet or low sample size (or to both). Nevertheless, we present our results by area to illustrate the substantial spatial variability of the diet of common dolphinfish in the EPO.

In the east area, the stomachs of 116 common dolphinfish were sampled from 1 dolphin set and 22 floating-object sets. Sixty-two of these stomachs were empty and 2 contained only trace hard parts (58.0% of the females, 52.5% of the males). The flyingfishes were the dominant prey in the east area in terms of all three indices (Fig. 4, east). Flyingfishes were eaten by 35% of the dolphinfish sampled and comprised 49% of the total weight of the stomach contents. Epipelagic cephalopods were also eaten by substantial numbers of dolphinfish (16% occurrence), and accounted for 24% of the prey counts. The epipelagic cephalopods were numerically important, but less so by weight, because their mandibles resist digestion and may accumulate in the stomachs over time. The other prey taxa were fairly rare in the east area.

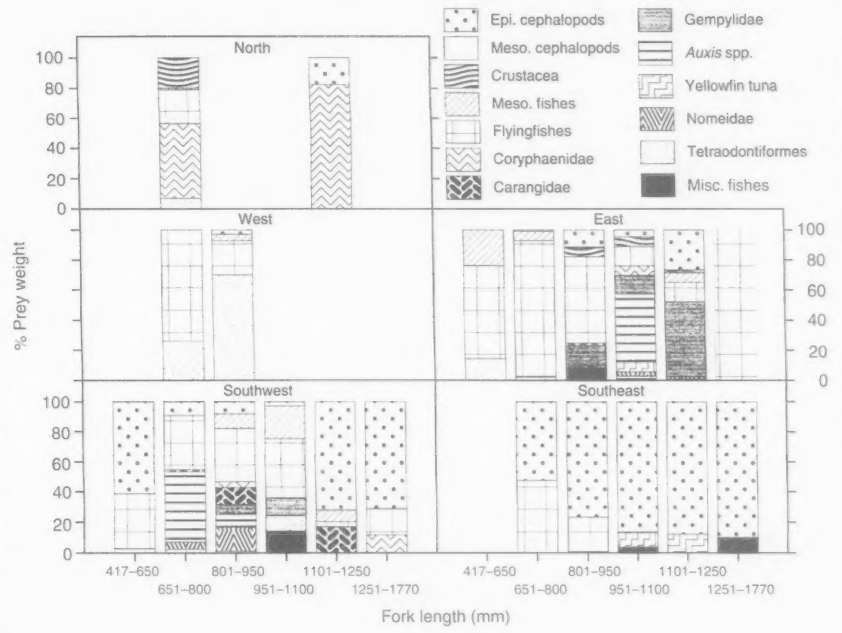

Figure 5

Gravimetric composition of prey groups (defined in Table 2), excluding trace quantities of hard parts, in the stomachs of 545 common dolphinfish sampled in five areas of the eastern Pacific Ocean (Fig. 1) versus dolphinfish size. Sample sizes for each size-area stratum are given in Table 1.

In the southwest area, the stomachs of 272 common dolphinfish were sampled from 2 dolphin sets, 5 schoolfish sets, and 22 floating-object sets. One hundred and thirty-six of the samples were empty and 14 contained only trace hard parts (60.1% of the females, 47.6% of the males). Flyingfishes and epipelagic cephalopods were found in 32% and 14% of the dolphinfish sampled, and also ranked first and second in biomass, respectively (Fig. 4, southwest). The dietary importance of both, as well as *Auxis* spp., was determined more by weight than by numbers of individuals, whereas the contrary was true for mesopelagic fishes. All the other prey categories were relatively rare in the diet according to all three measures.

In the southeast area, the stomachs of 115 dolphinfish were sampled from 1 schoolfish set and 13 floating-object sets. Fifty-two of the stomachs were empty and 7 contained only trace hard parts (44.6% of the females, 61.5% of the males). The epipelagic cephalopods were, by far, the dominant component in the diet in this area (Fig. 4, southeast). They were present in 45% of the stomachs sampled. Biomass and counts contributed about equally to the overall importance of epipelagic cephalopods in the diet. Flyingfishes also occurred in many of the samples (19%), but their contribution to the diet by weight and numbers was overshadowed by the epipelagic cephalopods. Four other diet categories were rare.

Size-specific predation

We present the prey composition in $\%W$, excluding trace quantities of hard parts (cephalopod mandibles and fish otoliths), by six dolphinfish size strata for five areas (Fig. 5). Sample sizes for each stratum are given in Table 1.

Considerable variability in the diet was apparent for common dolphinfish of different sizes. However, the statistical importance of size could be detected by the regression trees for only two prey groups because of the rarity of the other prey in the diet or because of small sample sizes. The regression tree for flyingfishes indicated that 7% of the apparent variation in the $\%W$ of these prey was explained by dolphinfish size. Size was also an important predictor of predation on Tetraodontiformes, explaining 9% of the apparent variation in the $\%W$ of these prey. Although dolphinfish size was not an important predictor of predation on the other prey categories, we present the feeding data by size strata within each area because we believe this variability is biologically important.

In the east area, the flyingfishes were the most important prey group overall for dolphinfish of the three smallest size classes and of the largest size class. For the two size classes between 951 and 1250 mm, frigate and bullet tuna (*Auxis* spp.), snake mackerels (Gempylidae), and epipelagic cephalopods were dominant (Fig. 5, east).

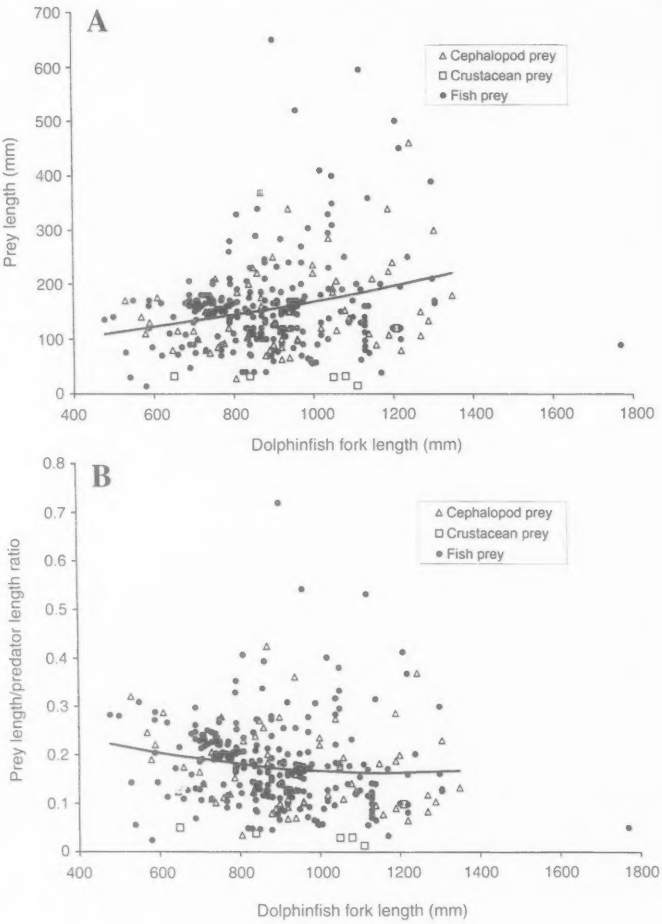

Figure 6

The length or maximum dimension of the prey (**A**) and prey relative sizes (**B**) versus dolphinfish size for three prey groups found in the stomach contents of common dolphinfish in the eastern Pacific Ocean. The lines represent the data smoothed with a smoothing spline, excluding the point for the largest dolphinfish.

In the southwest area, few large common dolphinfish were sampled (Table 1). The flyingfishes were important prey for the four smallest size groups (up to 1100 mm). Epipelagic cephalopods were important for the smallest and two largest size groups. *Auxis* spp. represented over 46% of the diet of dolphinfish between 651 and 800 mm fork length (Fig. 5, southwest).

In the southeast area, the epipelagic cephalopods dominated the diet (52–90%) of dolphinfish of all five size strata (Fig. 5, southeast). The flyingfishes comprised most of the remaining prey composition in the 651–800 and 801–950 mm categories, and *Thunnus* spp. (assumed to be mostly yellowfin tuna) comprised most of the remaining in the 951–1100 and 1101–1250 mm categories.

Prey size

We present the sizes of cephalopod, crustacean, and fish prey found in the dolphinfish stomach contents in Figure 6A. Intact prey ranged from 14 to 650 mm in length, and averaged 160 mm overall. The data smoothed with a smoothing spline showed an increasing trend of prey size with dolphinfish size. The maximum prey sizes increased gradually for dolphinfish up to about 760 mm, then abruptly to a maximum of about 600 mm for dolphinfish of approximately 1000 mm. This pattern was largely consistent for fish and cephalopod prey. Crustacean prey were small, but were consumed by a wide size range of dolphinfish.

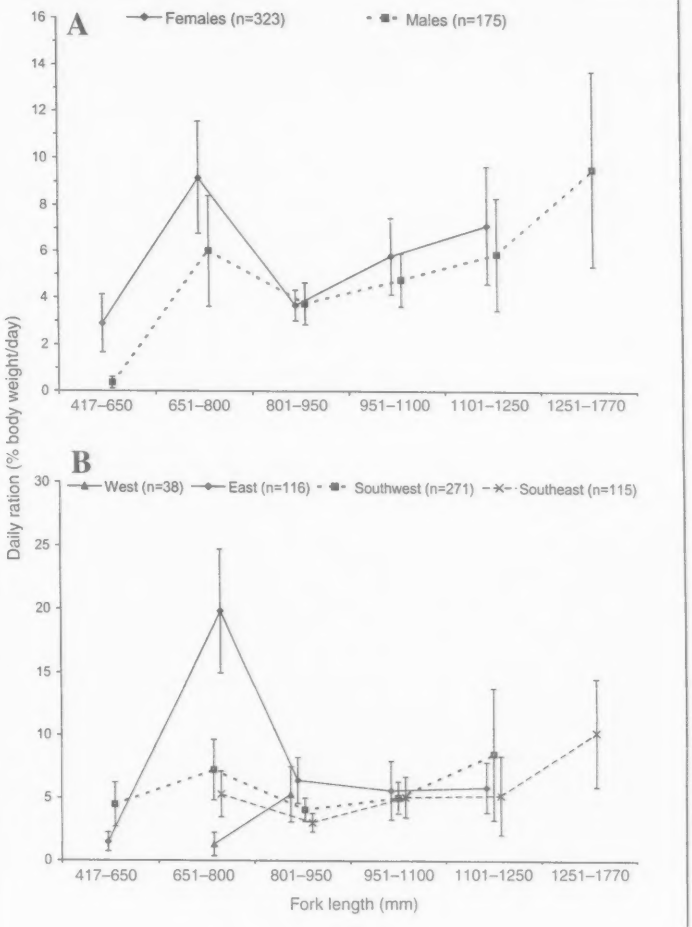

Figure 7

Mean (±1 SE) daily rations for six size strata of common dolphinfish, for all samples pooled by sex (**A**) and by area (**B**). Sample sizes are given in Table 1. Rations for some strata were not plotted if sample sizes were small (i.e. $n<5$).

The ratios of prey length to predator length ranged from 0.014 to 0.720, and averaged 0.177 (Fig. 6B). The length ratios, smoothed with a smoothing spline, showed a slight decreasing trend with dolphinfish size.

Consumption rates

The values of A_i (Eq. 1) chosen for the various prey taxa are listed in Table 2. We estimated a daily ration of 5.6 ±0.56% (mean ±1SE) of body weight per day for all common dolphinfish samples pooled. Mean ration estimates stratified by sex ranged from 0.4% of body weight per day for males of the smallest size group to 9.6% for males of the largest size group (Fig. 7A). Except for the 801–950 mm stratum, mean rations increased with dolphinfish size. Ration estimates were comparable for females and males, except for those in the smallest size stratum. The estimate for females in the 1251–1700 mm class was excluded from Figure 7A owing to a low sample size (n=2).

We present mean (±1 SE) daily ration estimates stratified by area in Figure 7B, if sample sizes were five fish or more. The calculations revealed that the 25 fish of the 651–800 mm group from the east area had ingested large amounts of food. These dolphinfish accounted for the high rations overall for both males and females of that size class (Fig. 7A). Except for that group and perhaps the 651–800 mm group in the west area, the ration estimates were comparable for all size classes in all areas (Fig. 7B). The number of empty stomachs did not unduly influence the consumption estimates by area. The percent of empty

stomachs (or containing only hard parts) ranged from 51% to 66% for the southeast, southwest, east, and west areas, respectively.

Discussion

Four previous studies of the food habits of common dolphinfish have been conducted in the EPO. Our results are difficult to compare meaningfully with those because they used different analytical techniques and had lower sample sizes. Larger sample sizes typically demonstrate greater trophic diversity (Manooch et al., 1983). Hida (1973) examined the stomachs of seven dolphinfish (two *C. hippurus* and five *C. equiselis*) caught at about 4°N–119°W. The largest component of the diet was flyingfishes (33%), followed by cephalopods (22%). Campos et al. (1993) sampled an unspecified number of *C. hippurus* caught off the Pacific coast of Costa Rica by experimental longline. Our results were similar to theirs in that flyingfishes was the most important component of the diet, and in both studies snake mackerel (Gempylidae) were found in the stomachs. Our samples from the east area, which encompasses the coastal waters of Costa Rica, contained more prey diversity, including mesopelagic fishes, portunid crabs, and penaeid shrimps. Campos et al. (1993) identified tuna of unknown species in the diet, and we found small amounts of predation on *Thunnus* spp. (yellowfin or bigeye tuna) in the east and southeast areas. Aguilar-Palomino et al. (1998) reported on the food habits of 500 *C. hippurus* caught by sport hook-and-line fishing in a small area at the tip of the Baja California peninsula, Mexico. They determined that the cephalopod *Dosidicus gigas* was the most important component of the diet, followed by the red crab *Pleuroncodes planipes*, a triggerfish, a flyingfish, and *Auxis* spp. Their results, however, could not be quantitatively compared with ours because they presented only the index of relative importance (IRI) (Pinkas et al., 1971), but not its three components (%*W*, %*N*, and %*O*). For example, it is impossible to determine if the apparent importance of *Dosidicus gigas* in their study was due to the presence of fresh biomass (i.e. high %*W*), the accumulation of numerous, small mandibles from previous meals (i.e. high %*N* and/or %*O*), or both. Likewise, the IRI indicated that small red crabs were important in the diet, but this index can be overly influenced by numerous small prey. We sampled only four dolphinfish in the north area near the south end of the Baja California peninsula and found some of the same prey taxa reported by Aguilar-Palomino et al. (1998). Lasso and Zapata (1999) analyzed the stomach contents of 228 *C. hippurus* using nonstandard methods. Their results were presented only by large categories, fishes, mollusks, and crustaceans.

Feeding periodicity

Our analysis of diel feeding periodicity suggests that, although common dolphinfish may be primarily visual predators (Massutí et al., 1998), they also feed at nighttime. Fish prey, such as flyingfishes, dolphinfishes, wahoo, and snake mackerel, would need to be ingested during nighttime hours to reach digestion states 3 or 4 before 09:00 hours the next morning, as we observed in our study, unless gastric evacuation rates are much faster than expected. Shcherbachev (1973) concluded from the presence of partially digested flyingfishes, myctophid fishes, and squids in the stomachs of *C. hippurus*, and crustacea in *C. equiselis* that dolphinfishes feed around the clock in the Indian Ocean. Rothschild (1964) described active feeding on flyingfishes and myctophids at night by *C. hippurus* in the central Pacific. Massutí et al. (1998) found that almost half of the stomachs of *C. hippurus* sampled at sunrise contained mesopelagic prey. Massutí et al. (1998) and Oxenford and Hunte (1999) also concluded that common dolphinfish feed at night, as well as during the day.

Our data analysis by area revealed an apparent relationship between the principal prey taxa in the diet and feeding periodicity. In the southwest and southeast areas, recently eaten cephalopods were in the stomachs throughout the daytime sampling period, although no samples were taken in the southeast in the late afternoon (Fig. 3). In contrast, in the east area the dolphinfish preyed mostly on fishes (flyingfishes, *Auxis* spp., and gempylids) that require more time than cephalopods for gastric evacuation (Olson and Boggs, 1986). In the east area, recently eaten prey were present only in the early morning and early afternoon, and the food remains in the late morning and late afternoon were in advanced stages of digestion. These results suggest that foraging activity may have been influenced by the digestibility and energy content of the available prey. Cephalopods are typically low in energy content, whereas fishes store lipids in the musculature and viscera and have higher energy densities (Cummins and Wuycheck, 1971). Grove et al. (1978), Flowerdew and Grove (1979), and Jobling (1981) demonstrated that low-energy foods are emptied from the stomach more rapidly than foods of higher caloric content. Elevated lipid content in natural organisms is thought to have a retarding effect on gastric evacuation (Fänge and Grove, 1979). In yellowfin tuna, gastric evacuation rates were inversely correlated with total lipid content of four food organisms (Olson and Boggs, 1986). Apparently, the dolphinfish in the southwest and southeast areas spent more time foraging to fulfill their energy requirements than the dolphinfish in the east area.

Diet considerations

Our study indicated that only two prey groups, flyingfishes and epipelagic cephalopods, were dominant in the diet of common dolphinfish in the EPO (Fig. 4).

Diet differences we attributed to spatial stratification also had a seasonal component. Of the stomach samples obtained north of the equator in the north, west, and east areas, most (85%) of those that contained fresh food, were caught from May through November. The trends described for common dolphinfish in the southwest and southeast areas may also have been attributable to seasonality of the prey from December through April because all the dolphinfish in these areas were caught during these months.

The marked differences in food habits with predator size are noteworthy. For all areas combined, the general trend was for increased predation on cephalopods and decreased predation on flyingfishes as the dolphinfish grew larger. The exception was the smallest size group (417–650 mm). These dolphinfish ate 50% cephalopods and 40% flyingfishes by weight. Zavala-Camin (1986) also found greater predation on cephalopods by large dolphinfish (>850 mm) than by smaller specimens off Brazil.

Piscivores are known to feed selectively according to prey body size (Tonn et al., 1992). Maximum prey size is determined by the mouth gape of the predator (Magnuson and Heitz, 1971; Hambright, 1991), and minimum prey size was correlated with the gap width between the gill rakers for a variety of tunas, mackerels, and dolphinfishes (Magnuson and Heitz, 1971). Preference for the largest prey a predator can ingest is supported on theoretical grounds (Ivlev, 1961; Harper and Blake, 1988), but a survey of studies examining prey-size selectivities of piscivorous fishes showed a consistent pattern of selection for small prey (Juanes, 1994). In our study, the common dolphinfish of all sizes ingested small prey (Fig. 6A). Ratios of prey size to predator size for piscivores tend to average 0.2–0.3 (Juanes, 1994). In our study, the dolphinfish ingested prey that averaged slightly smaller, 17% of their length. A few dolphinfish ate prey that were greater than the maximum reported for piscivores, 50% of their length (Juanes, 1994).

Consumption rates

The method we employed for estimating daily rates of food consumption was judged by Cortés (1997) to be among the two most appropriate methods for top predators. However, applying gastric evacuation rates derived for yellowfin tuna to estimate daily rations of common dolphinfish requires justification. Suzuki's (1992) observations of gut-evacuation times of small dolphinfish do not unequivocally justify our assumption that gastric evacuation rates are comparable to those of yellowfin tuna, which were based on food passage through the stomach alone. However, energetics requirements suggest that gastric evacuation times for dolphinfish, at the same temperature, would be on the order of those for yellowfin. Our hypothesis is supported by the similar standard metabolic rates of common dolphinfish and yellowfin (Benetti et al., 1995; Brill, 1996). Brill (1996) argued that high rates of digestion are consistent for high-performance fishes like tunas, billfishes, and dolphinfishes and demonstrated that dolphinfishes share several characteristics of high-performance physiology with tunas and billfishes. Other, similar-size teleost fishes require about five times as long as yellowfin and skipjack to evacuate a meal (Magnuson, 1969; Olson and Boggs, 1986). Until gastric evacuation rates of dolphinfish are measured, we are confident that our first-order estimates are adequate approximations of daily rations of common dolphinfish in nature.

Our ration estimates for common dolphinfish are greater than those for yellowfin tuna of comparable size, estimated by the same method (Olson and Boggs, 1986; Olson and Mullen, 1986). Our estimates are consistent with the observation that, although standard metabolic rates and locomotion costs are comparable for these species, common dolphinfish have greater growth rates than yellowfin (Uchiyama et al., 1986; Wild, 1986) and may require more energy for growth.

In summary, dolphinfish are an important component of the pelagic food web in the EPO, and as such, their feeding ecology provides clues to the underlying ecosystem structure. Clearly, *C. hippurus* imparts predation pressure on cephalopods, flyingfishes, and other prey that are shared by a suite of predators (Juhl, 1955; King and Ikehara, 1956; Blunt, 1960; Perrin et al., 1973; Nakamura, 1985; Olson and Boggs, 1986; Robertson and Chivers, 1997; Markaida and Sosa-Nishizaki, 1998). This predation pressure lends support to the hypothesis that cephalopods and flyingfishes are abundant or have high ratios of production to biomass (P/B) (or both) in the EPO. This hypothesis is based on 1) high consumption rates on these prey, indicated by the stomach contents in our present study, 2) high P/B of dolphinfish (Oxenford, 1999), 3) high consumption rates of cephalopods and flyingfishes by other predators (cited above), and 4) high P/B of those predators (Boggs, 1989; IATTC, 1999). This analysis illustrates the importance of diet studies for providing ecological insights.

Our study provides key data for implementing ecosystem analyses based on food-web models (Christensen and Pauly, 1992; Walters et al., 1997). For example, *Ecopath with Ecosim* (www.ecopath.org) requires data on both the diet compositions and consumption rates of predators. Accordingly, we summarized the prey data by several levels of taxonomic resolution and functional groups for dolphinfish sampled at multiple spatial scales and size classes. These data help lay the groundwork for a community- and ecosystem-level approach to fisheries management in the EPO.

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Recruitment season, size, and age of young American eels (*Anguilla rostrata*) entering an estuary near Beaufort, North Carolina

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Abstract–Net catches from 1985–86 to 1994–95 at Pivers Island, North Carolina, indicated that glass-eel stage American eels (*Anguilla rostrata*) were recruited to the estuary from November to early May, with peak numbers in January, February, and March. There was no declining trend in recruitment over the years of sampling. Except for one year, there was no clear seasonal decrease in mean length. But shorter glass eels were older than longer glass eels, as judged by age within the glass eel growth zone of the otolith, suggesting that smaller fish took longer to arrive. The mean age of glass eels collected from the lower estuary and a freshwater site 9.5 km upriver differed by 8.4 d (36.2 vs. 44.6, respectively). Outer increments (30–35) of the otolith growth zone of glass eels from North Carolina were significantly wider than corresponding increments of otoliths from New Brunswick. Mean total ages of North Carolina, New Jersey, and New Brunswick elvers were 175.4, 201.2, and 209.3 d, corresponding to mean lengths of 55.9, 60.9, and 58.1 mm TL, respectively. The mean durations of glass-eel growth zones (44.6, 62.3, and 69.8) were in close agreement with those from previous studies, but total ages were not. This suggested that perhaps some finer (leptocephalus stage) increments were not detected by light microscopy, differences occurred in seasonal increment deposition, or absorption of the otolith material may have taken place during metamorphosis, rendering the aging of larvae inaccurate. Judging from the long recruitment period and seasonal uniformity in both mean age and length found in our study, the spawning period of American eels may be somewhat more protracted than previously considered.

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The life history of the American eel (*Anguilla rostrata*) is both fascinating and mysterious. It spawns in the Sargasso Sea and the young willow leaf-shaped leptocephalus larva disperses over great distances before it metamorphoses into a transparent glass eel. This stage reaches the estuaries of North America where it typically ascends rivers and streams as an elver, becoming progressively more pigmented as the run progresses. This stage is followed by the juvenile or yellow eel, and finally by the silver or maturing adult (Able and Fahay, 1998). Eel physiology and ecology are still not completely understood, although much has been learned since the early 1900s. Schmidt (1922) discovered the general area of spawning in the Sargasso Sea, and Kleckner et al. (1983) further demarcated breeding to an area defined by thermal front boundaries. Comparini and Rodino (1982) used electrophoretic analysis on American and European eel (*Anguilla anguilla*) leptocephali to confirm that both spawn in the Sargasso Sea.

Based on oceanographic surveys and entrance times into rivers, estimates of migration time to North America of young *A. rostrata* range from 250 days to one year, corresponding with a peak spawning time of February and March (McCleave et al., 1987; Haro and Kreuger, 1988). Many studies have described seasonal sizes of European glass eels and elvers entering estuaries, but similar long-term data sets for the American species are uncommon. Elvers enter estuaries along the coast of North America progressively from south to north, becoming larger with increasing latitude (Haro and Kreuger, 1988), and for many (but not all) areas, sizes have been recorded. We document the recruitment period and variations in its seasonality for the Beaufort, NC, region for the 1985–86 to 1994–95 seasons.

Michaud et al. (1988) documented the sizes but not the ages of American eel elvers entering a Quebec river. Jessop (1998) used large samples from the Nova Scotian elver fishery to show seasonal declines in length and weight and an increase in pigmentation of newly arrived elvers. Wang and Tzeng (1998) used SEM (scanning electron microscopy) and elemental analysis of otoliths to determine ages of elvers taken from Haiti, north to Nova Scotia. They also estimated the length in days of the leptocephalus and glass-eel stages from the same sites. Helfman et al., (1984) described the length range of glass eels entering a Georgia river in February. Although most earlier workers (e.g. Vladykov, 1966; Eldred, 1968, and others) did not have long-term data series, their samples are useful for comparisons with current data.

Long-term records of estuarine recruitment of early life-history stages of eels are particularly relevant at this time, when reduction in juveniles (but not elvers) to the upper St. Lawrence River area in North America has been noted (Castonguay et al., 1994a), and when catches of adults and recruitment of elvers are declining in Europe (Castonguay et al., 1994b). We therefore present subsamples of ages along with our catch per effort (densities) for glass eels. Earlier studies of eel otoliths used SEM to determine ages, but we used light microscopy for comparison with such studies. Castonguay (1986) aged *A. rostrata* leptocephali captured in the Gulf of Maine, and his largest individual of 49 mm TL (which would shrink during metamorphosis) was 130 d. However, only the daily growth increments in the elver growth zone (area after the "transition" or "elver" check) have been validated (Martin, 1995). He validated daily increments in the field over a one-month period. Lecomte-Finiger (1992) aged otoliths of *A. anguilla* elvers from several European locations, as did Antunes and Tesch (1997). The latter suggested that daily increments of *A. anguilla* may be underestimated because of the "diffuse" (their term) nature of the metamorphosis zone. More recently, Cieri and McCleave (2000) suggested that there are a number of inconsistencies when growth zones of leptocephali are compared with the same zone in the otoliths of glass eels and juvenile American eels. Both radii and ages were less in the older fish stages than in the leptocephali. The possibility of resorption of otolith material during metamorphosis (and subsequent obliteration of increments) led them to discourage the use of larval eel otoliths for aging or back-calculating life history events until these discrepancies could be explained. Although the present authors could not validate increments in the leptocephalus stage or metamorphosis stage (these stages metamorphose before reaching North Carolina), we collected samples to temporally validate daily increments in the glass-eel stage. We tested the hypotheses that 1) the increment number for glass eels at an upriver (freshwater) location would be greater than that for glass eels at a lower (estuarine) sampling site by a difference (in days) equal to the distance divided by the sum of the swimming speed and tidal transport, and that 2) increment widths for corresponding glass-eel portions of the otolith for fish from the Bay of Fundy (New Brunswick sample) would be narrower than for fish of warmer water (i.e. North Carolina) because the warmer waters would produce faster growth which, in turn, could produce wider otolith increments. A New Jersey sample was also aged to represent an intermediate geographic position between North Carolina and New Brunswick.

The objectives of this study were 1) to describe the 1985–95 annual recruitment of glass eels to the estuary near Beaufort; 2) to present the variations in seasonal densities of glass eels; 3) to analyze the seasonal length frequency by weekly intervals, and 4) to compare mean ages of glass eels at three locations along the eastern coast of North America (North Carolina, New Jersey, and New Brunswick). We also tested two hypotheses relevant to validating daily deposition of otolith growth increments in the glass-eel stage of *Anguilla rostrata*.

Methods

Collections

Glass eels were collected from two sites in North Carolina: 1) in the lower Newport River at Pivers Island, about 2 km inside Beaufort Inlet; and 2) at Black Creek, a small tributary of the Newport River, at the entrance to a millpond, about 9.5 km upriver from Beaufort, North Carolina. The samples at Pivers Island were collected over the 10-year period 1985–95 with a 1×2 m neuston net fitted with 945-um mesh and flow meter and suspended from a bridge, except during 1985–86, when 60-cm bongo nets were used. Details of the sampling protocol are given in Warlen (1994). Samples were always collected at night during midflood tide, from November to April. Density of fish in the catches was standardized as the mean number per 100 m^3. Additional samples were collected by dip net from Black Creek just below a small dam leading into a millpond (22 February and 20 March 1994). Samples were also obtained from two areas north of North Carolina: 1) Little Egg Inlet, New Jersey, at the site of the Marine Field Station, State University of New Jersey, Rutgers,Tuckerton, NJ (39°30′N, 74°14′W) on 21 Februrary and 9 March 1994 (with a 1-m plankton net); 2) elvers were captured from the Lepreau River, at the village of Lepreau, New Brunswick, Canada, on the Bay of Fundy (45°00′N, 66°20′W) on 6 June 1994. This sample was collected with a 1-mm mesh dip net and was preserved in 70% ethanol. All other samples were preserved in 95% ethanol, and then preserved in fresh 70% ethanol after 24 h.

Aging methods

All eels were measured (TL to the nearest 0.1 mm) with a Vernier caliper and saggital otoliths were removed, washed, dried, and mounted on glass slides with thermal cement, sulcus groove down. The otoliths were ground with a series of wet grit papers (no. 600 to 1200) until the core was visible, then polished with diamond paste, after which they were aged by using an oil-immersion lens from 1200 to 3100×. A subsample of 10 otoliths was also sectioned (transverse) and prepared for reading, and ages were compared with ages from whole otoliths from the same fish. Sectioned otoliths had about 4% more rings in the outer edge. Otolith increments were read from the hatching ring outwards, as suggested by Lecomte-Finiger (1992) and Tzeng (1996). Umezawa and Tsukamoto (1991) found that no rings were formed during the incubation period (5 days) of *A. japonica*. To maintain consistency with other authors, we therefore added five days to our ages. An optical imaging system was used to count increments and to measure increment widths and the distance from the core to the first-feeding (exogenous) ring, etc. The lowest increment width (distance between adjacent dark rings) recorded was 0.326 µ, a distance which was probably close to the resolution minimum of our microscope. Incremental counts were made of the leptocephalus growth zone, the metamorphic zone, the glass-eel growth

zone, and from the "elver" check (transition mark) to the edge of the otolith (see Cieri and McCleave, 2000). Total ages were estimated as the age from the hatching ring to the elver mark. Glass-eel growth zone ages (increments from the outer boundary of metamorphic zone to elver check) were read as in Wang and Tzeng (1998).

Age studies

The mean ages in the glass-eel growth zones of eels taken at Pivers Island in February were compared with mean ages in glass-eel growth zones of eels taken at an upper estuary site, the Black Creek Mill Pond entrance (also in February). The difference in mean age presumably reflected the time required to travel the distance upriver to the collection site.

The total ages and the ages found in the glass-eel growth zone were compared with those for small and larger glass eels arriving during the recruitment season. Glass eels were divided into length groups (from 46.1–48.0 TL to 58.1–60.0) and corresponding age frequencies were assigned to each length group. A linear regression was then fitted to the data to assess whether or not smaller fish were older or younger than the longer members of their recruitment class.

Statistical analysis

Seasonal trends in the weekly length distributions were examined by linear regression (SAS Institute, 1996) for each sampling (recruitment) season, and for the whole 10-year period (1985–86 to 1994–95).

The differences in otolith increment widths in the early (proximal) glass-eel growth zone (increments 10–15) and later (mid-distal) glass-eel growth zone (increments 30–35) from the New Brunswick and North Carolina samples were examined by analysis of variance (ANOVA). Age distributions of glass eels captured by month were compared by using the F-test. Statistical significance was accepted at $P < 0.05$.

Results

Annual recruitment

The total density of glass eels in the Beaufort estuary varied considerably between 1985 and 1995, but there was no significant trend (F_8=1.605, adj r^2=0.123, slope=–0.031, P=0.246) among the 10 consecutive recruitment years in the Beaufort estuary (Fig. 1). Densities were highest in 1988–89 and 1993–94 (13.5–14.0 eels/100 m^3) and lowest in 1990–91 (1.5 eels/100 m^3), a ninefold difference. Apart from the low of 1990–91, all other years had total densities of more than seven eels/100 m^3. After the 1990–91 low, the total annual density of elvers at Beaufort increased again (F_3=4.88; slope 2.04, r^2=0.78, P=0.113), approaching the previous mean level.

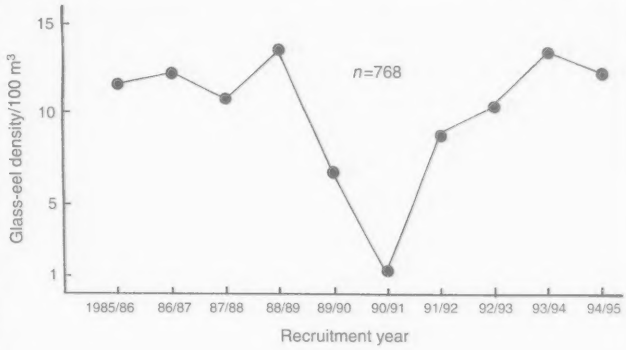

Figure 1

Mean density of *Anguilla rostrata* glass eels (no. of eels/100 m^3) caught each year, from 1985–86 to 1994–95, between November and April at Pivers Island, Beaufort, North Carolina.

Seasonal recruitment

Although glass eel recruitment sometimes occurred over a 5 1/2 month period (mid-November to early May), most recruitment of young eels to the estuary occurred from December through April (Fig. 2). Although there was some variation among years within the recruitment period, the largest catches usually occurred in February and March. Peak catches varied from early in the season (1985–86) to late in the season (1987–88). In 1993–94, densities were highest in mid-January and mid-March. In (1990–91), the year with the lowest catches, almost all of the catch occurred in December and January, with virtually none afterwards.

When seasonal changes in length of glass eels among recruitment years were analyzed (Table 1), the slope of the regression for all 10 years (Fig. 3) was positive, but not significant (F_1=19.50, P=0.001). Four seasons had negative regression slopes and slopes for the other years were positive, three of which were significant.

Age studies

The mean age observed in the glass-eel growth zones of eels collected in February from the Pivers Island and Black Creek sites differed significantly, by eight days (F_2= 6.651, P=0.003). The Pivers Island eels averaged 36.2 d (52.9 ±0.9 mm TL) for their as yet uncompleted glass-eel phase, and the Black Creek elvers averaged 44.6 d (55.9 ±0.9 mm TL). The distance between the two sites was about 9.5 km.

In respect to otolith growth, the mean widths of the first 10–15 daily growth increments in the glass-eel growth zone (Table 2) were not significantly different (F_2=1.363, P=0.185) between the northern eels (New Brunswick) and the southern eels (North Carolina). However, both samples of otoliths from North Carolina indicated that mean

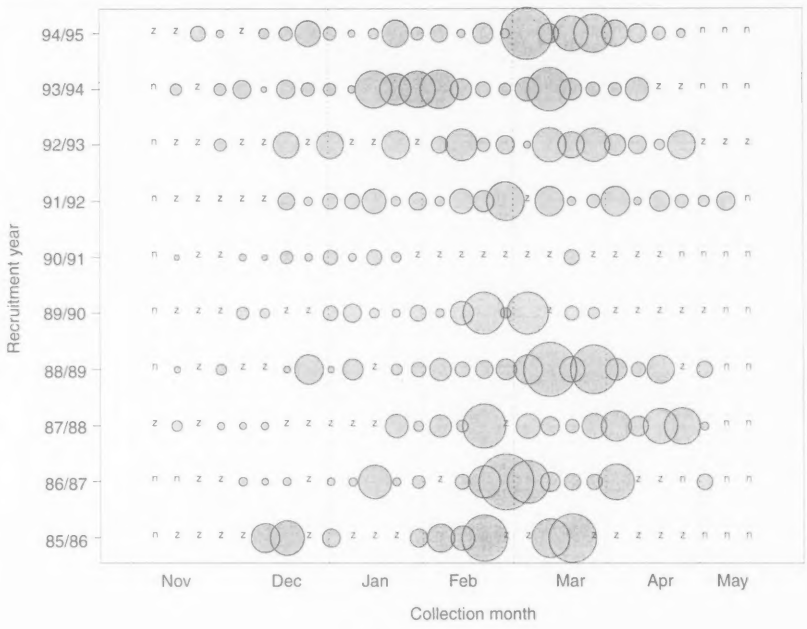

Figure 2

Total densities of *Anguilla rostrata* glass eels (no. of eels/100 m^3) by week during recruitment seasons, from 1985–86 to 1994–95. Larval density is proportional to circle area: smallest density (0.034) at week 2 of season 1990–91; largest density (3.690) at week 17 of 1986–87 season. *n* = no sampling and *z* = sampling with zero catch.

Table 1

Linear regression coefficients for total length on collection week for glass-eel stages of American eel taken at Pivers Island, Beaufort, North Carolina, in each of 10 recruitment seasons, with 95% confidence intervals for slopes and intercepts. *P* is the probability of failing to reject the H_0 All years: $Y = 52.15 + 0.088X$ (r^2=0.026).

Recruitment year	*n*	Adjusted r^2	Intercept	Slope	*F*	*P*
1985–86	34	0.19	48.92 ±3.48	0.24 ±0.15	1.58	0.245
1986–87	61	0.03	50.87 ±2.94	0.15 ±0.14	2.87	0.095
1987–88	73	0.11	50.63 ±2.49	0.19 ±0.12	10.21	0.002
1988–89	81	0.02	52.65 ±2.41	0.09 ±0.07	2.27	0.136
1989–90	48	0.00	54.45 ±2.80	–0.09 ±0.08	1.03	0.315
1990–91	15	0.07	53.18 ±5.24	–0.01±0.39	0.00	0.958
1991–92	60	0.33	48.82 ±1.70	0.27 ±0.10	30.66	0.001
1992–93	60	0.01	54.11 ±4.00	–0.07 ±0.07	1.37	0.247
1993–94	18	0.02	54.94 ±1.48	–0.09 ±0.09	3.70	0.057
1994–95	132	0.01	52.97 ±1.55	0.07 ±0.08	2.40	0.124

incremental widths (1.717 and 1.732) in the later stage of the glass eel (increments 30–35), were wider (F_2=3.93 , *P*=0.004) than the corresponding mean width (1.314) for New Brunswick otoliths, as hypothesized, suggesting faster growth in the southern waters.

The youngest (mean 168 d) American eel elvers were found at the Pivers Island site (Table 3), whereas elvers at Black Creek (just north of Pivers Island) were not significantly different at age 175 d (F_2=1.125, *P*=0.376). Neither elvers from New Jersey (201 d) nor those from New

Table 2

Mean increment widths (microns) with 95% confidence limits in the glass-eel growth zone of *Anguilla rostrata* otoliths from three different sampling sites and the number showing the "elver" or "transition" mark. Number in sample (n) applies to both increment groups. Means without a letter in common (y and z) were significantly different ($P \leq 0.05$).

Sample site	n	Width (μ) of 10–15th increment	Width (μ) of 30–35th increment	Presence of elver mark (%)
Pivers Island, North Carolina	77	1.425 ±0.114 z	1.717 ±0.189 z	0
Black Creek, North Carolina	27	1.330 ± 0.169 z	1.732 ±0.180 z	93
Lepreau, New Brunswick	43	1.232 ±0.168 z	1.341 ±0.163 y	98

Table 3

Means (±SD) for total age, glass-eel age, and total length (TL) for young eels, *Anguilla rostrata* collected in our study. Only glass-eel ages were significantly different (*) between locations (F-test, $P \leq 0.05$). n = number of otoliths analyzed.

Location	Date	n	Total age (d)	Glass eel age (d)	Length (TL mm)
Pivers Island, North Carolina	Dec–Apr 1985–94	77	167.2 ±16.9	36.2 ±3.2*	52.9 ±2.4
Black Creek, North Carolina	2–23 Feb 1994	25	175.4 ±12.6	44.6 ±1.6*	55.9 ±3.1
Little Egg Inlet, New Jersey	Feb–Mar 1994	22	201.2±16.1	62.3 ±8.8*	60.9 ±3.0
Lepreau, New Brunswick	6 June 1994	43	209.3±18.1	69.8 ±10.5*	58.1 ±3.8

Table 4

Regression of collection week (1–26) against total age in days (with 95% confidence limits) and regression of glass-eel growth zone age (outer metamorphic zone to elver check on otolith) against total length (mm) for glass eels collected at Pivers Island, North Carolina. The sampling period (recruitment season) extended from November to mid-May, 1985–86 to 1994–95. n = number of otoliths analyzed.

	n	Slope	Adjusted r^2	Intercept	P	Mean age
Collection week against total age	89	0.339	0.053	170.2	0.976	173.1 ±2.7
Glass eel growth zone age against total length	89	– 0.311	0.499	77.5	0.014	60.6 ±1.7

Brunswick (209 d) were significantly older than those from North Carolina (F_2=1.111, P=0.407; F_2=1.140, P=0.373) with respect to total age. Although New Jersey fish appeared to be longer (60.9 mm TL) than New Brunswick elvers (58.1 mm TL), the difference in mean length was not significant (F_2=1.283, P=0.266).

Although total mean age (d) counts were not significantly different between sites (Table 3), glass-eel age (the portion between metamorphosis zone and elver mark of otolith) differed between all three sites (NC vs. NJ, F_2= 7.713, P=0.005; NJ vs. NB, F_2=1.622, P=0.091). Furthermore, when glass-eel ages were regressed against latitude, the relationship was significant (slope=0.303, adj. r^2=0.835, P=0.028).

In light of Jessop's (1998) finding of a decrease in length over the recruitment season for elvers in the Bay of Fundy waters, we re-examined our age data by month and length. Could it be that even though our lengths showed no significant seasonal decrease, shorter fish were, on average, older than longer fish? The regression of the capture date against total mean age suggested an increase in age over time (Table 4), but the relationship was weak (adj. r^2=0.053). Furthermore, an F-test revealed no difference in incremental total age between any month. But total age is apparently not to be trusted (Cieri and McCleave, 2000). When we regressed mean length against only the glass-eel zone age, it revealed just the opposite relationship: a negative slope (Table 4), with a good relationship (adj. r^2=0.499). The smaller fish during the recruitment period were indeed older, as suggested by Jessop (1998). The longer fish, on average, had fewer increments in their glass-eel growth zone than the shorter fish, suggesting that the latter had taken longer to reach Beaufort estuary from the Sargasso Sea.

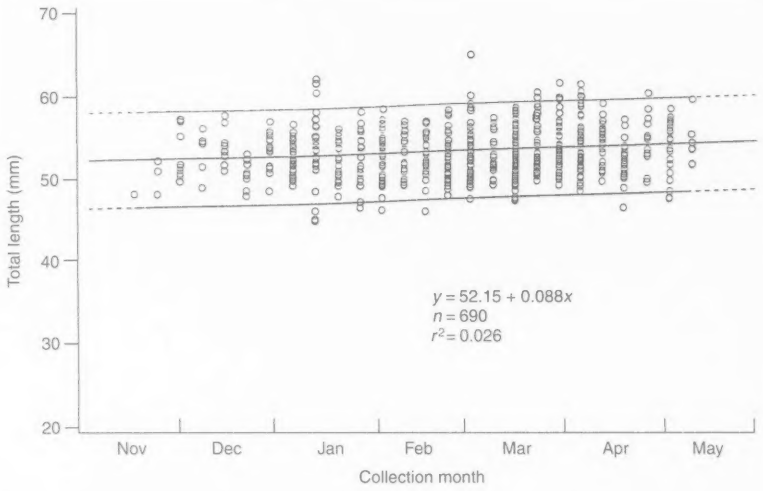

Figure 3

The regression of total length on week of capture for *Anguilla rostrata* glass eels collected at the Pivers Island bridge during 10 recruitment seasons from 1985–86 to 1994–95. Boundary lines represent 95% confidence limits.

Discussion

Glass eels were recruited to the Beaufort estuary over a 7-month period from November to early May during the ten years from 1985–86 to 1994–95. Peak recruitment occurred in February–March of most years. Catch distributions were usually skewed, either positively or negatively, and clumped. Variation in estuarine recruitment time may have been due to differences in oceanic transport rates for larvae, and perhaps to slight differences in times of peak spawning, a well-known phenomenon in many other fish species. Able and Fahay (1998) also found that most glass eels recruited to a New Jersey estuary from January to June (in 1991 to July), with peaks usually in February and March. In Nova Scotia the main fishery for elvers in 1997 extended from late April to mid-August (Jessop, 1998). The recruitment period for the two southernmost localities and Nova Scotia thus overlapped in April and May: as the North Carolina and New Jersey recruitment period ends, the northern Bay of Fundy area typically commences.

Although there was a large variation in the numbers of eels caught among years, there was no indication of an overall reduction in recruitment. Castonguay et al. (1994b), and Marcogliese et al. (1997) have suggested a number of possible reasons for a decline of European eels, but such a decline was not reflected in our catches of elvers at Beaufort. Jessop (1997) also concluded that there had not been a decline in elvers recruited to Atlantic coastal waters of the Canadian maritime provinces over the past decade (last year 1996).

The lengths of elvers captured in the tidal net at Pivers Island fell within the expected latitudinal length range reported by Haro and Kreuger (1988) and were similar to the 49–56 mm TL length range for glass eels from a river in Georgia (Helfman et al., 1984). Mixed elvers and small juveniles (not aged) in the Great Bay area of New Jersey, from 1986 to 1994 averaged 60–90 mm TL (Able and Fahay, 1998). Elvers collected by Jessop (1998) in 1997 in the Bay of Fundy waters ranged from 52.0 to 70.0 mm TL (considerable variation was evident among rivers of New Brunswick and Nova Scotia.). Even farther to the north (Quebec), Michaud et al. (1988) reported lengths of elvers for 1987 from the St. Lawrence River estuary to extend from 50 to 70 mm TL. Comparing our data with that of other studies, and allowing for 2.8% shrinkage in length of our eels (unpubl. data) due to alcohol preservation (our samples), as opposed to 1–2% shrinkage in 6–10% formalin (Jessop, 1998; Stobo, 1972), we found that there was a remarkable consistency in the clinal length ranges from north to south. Some inconsistency was expected because we compared studies in which sampling was done at both river mouths and estuaries, where it is known that ascent up rivers is usually dependent upon temperature or stream level (Martin, 1995; Jessop, 1998).

In a study of the Bay of Fundy waters, Jessop (1998) showed that as the season progressed, lengths of young eels entering most, but not all, rivers declined to a maximum of 7%. The length of recruiting European eel elvers also declined seasonally (Cantrelle, 1981). Yet our combined length-frequency plot of all fish collected over the ten-year period showed a nonsignificant regression. It may be that only elvers to the north of our location show a definitive decrease in lengths over time or that our samples were too small to confirm the phenomenon.

The difference in estimated mean age of 8 days from glass-eel growth zones at two North Carolina locations about 9.5 km apart implies that upriver movement was about 1 km a day, much of which could be tidal. We do not know whether or not this rate of movement is reasonable or typical.

The mean age from our glass-eel growth zones on otoliths of glass eels agreed with the ages determined from other glass eels collected in North Carolina (Wang and Tzeng, 1998).

Finally, the apparent total ages and glass-eel ages from North Carolina, New Jersey, and New Brunswick support the hypothesis that eels are progressively older to the north, and are consistent with their greater distance from the Sargasso Sea.

Total age estimates of glass eels can be compared with those from two other studies of American eel. Our average total age of glass eels from Black Creek (175 d) was 14% older than the 153 d that Budimawan (1996) found for the same location, date, and year. On the other hand, estimated total ages of glass eels were considerably less (20–22%) than the ages obtained by Wang and Tzeng (1998) for eels from the same general areas (but different dates). Because ages from glass-eel growth zones (as opposed to total age) were in very close agreement with those of Wang and Tzeng (1998), one assumption for this inconsistency in total age is a difference in interpreting age in either the leptocephalus or metamorphic zone. It is also possible that increments ≤0.3 µ wide may not have been distinguishable by light microscopy, which could account for our ages being younger than those of Wang and Tzeng (1998), who used SEM. Antunes and Tesch (1997) have also suggested that these two methods of otolith observation may produce different results. It is conceivable that increments in the leptocephalus growth zone may be laid down in fewer numbers in some seasons, but it seems unlikely that low water temperatures would cause a cessation of otolith increment deposition, because the Gulf Stream top 200-m layer (the assumed habitat of leptocephali) maintains an annual temperature above 16°C (Stommel, 1965). Absorption of increments during metamorphosis (Cieri and McCleave, 2000) is possible, but our studies could not shed any light on this proposed phenomenon because all leptocephali had metamorphosed before reaching North Carolina. Obviously, there is consistent agreement among authors in incremental counts of glass-eel growth zones, which are wide and clear, and therefore easy to count.

Regardless of the discrepancy in age estimates of larval eels, evidence from the rate of transport of other species in the Gulf Stream suggests that once they have reached the Gulf Stream, it is possible for leptocephali to reach the continental shelf of North Carolina in about 110 days. A NOAA (National Oceanic and Atmospheric Administration) sea drifter released in 1996 west of the western edge of the Sargasso Sea in 1996 and travelling just inside the western front of the Gulf Stream at 100 m depth reached the North Carolina outer continental shelf in 50 days. Its release site appears to overlap stations where leptocephali of *A. rostrata* were captured (Wippelhauser et al., 1985; Kleckner and McCleave, 1985). Larvae of several fish species from Florida waters are known to reach the area offshore North Carolina in 25–30 d (Hare and Ahrenholz).[1] For example, larval Atlantic menhaden (*Brevoortia tyrannus*) that spawned offshore from Beaufort in an area close to the path of the sea drifter reached the estuary near Beaufort, North Carolina, in an average of 60 d (Warlen, 1994). This estimate of across-continental shelf transport, when added to the 50 d of travel for the sea drifter, gives an elapsed time of 110 d. This estimate of transport duration may prove to be useful in the future.

McCleave et al. (1998) surmised that leptocephali of the European eel (virtually identical in physical structure to *A. rostrata*) do not actively swim toward land during their migration to Europe. Granted that the age increments in the larval zone of the otolith of American eels may not accurately depict early life-history duration (Cieri and McCleave, 2000), the consistency of recruited lengths and glass-eel ages over the years from 1985 to 1995 is noteworthy. In addition, the annual recruitment seasons and sizes observed in coastal North Carolina and New Jersey regions (Able and Fahay, 1998) reveal a remarkably consistent sequential latitudinal pattern. It appears that current data on seasonal recruitment of young eels should continue to be used to examine temporal relationships between geographical areas and oceanic transport times from the spawning area (Sargasso Sea) to the estuaries.

Acknowledgments

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Changes over time in the spatial distribution of walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska, 1984–1996

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Abstract–Triennial bottom trawl survey data from 1984 to 1996 were used to evaluate changes in the summer distribution of walleye pollock in the western and central Gulf of Alaska. Differences between several age groups of pollock were evaluated. Distribution was examined in relation to several physical characteristics, including bottom depth and distance from land. Interspecies associations were also analyzed with the Bray-Curtis clustering technique to better understand community structure. Our results indicated that although the population numbers decreased, high concentrations of pollock remained in the same areas during 1984–96. However, there was an increase in the number of stations where low-density pollock concentrations of all ages were observed, which resulted in a decrease in mean population density of pollock within the GOA region. Patterns emerging from our data suggested an alternative to MacCall's "basin hypothesis" which states that as population numbers decrease, there should be a contraction of the population range to optimal habitats.

During 1984–96 there was a concurrent precipitous decline in Steller sea lions in the Gulf of Alaska. The results of our study suggest that decreases in the mean density of adult pollock, the main food in the Steller sea lion diet, combined with slight changes in the distribution of pollock (age-1 pollock in particular) in the mid-1980s, may have contributed to decreased foraging efficiency in Steller sea lions. Our results support the prevailing conceptual model for pollock ontogeny, although there is evidence that substantial spawning may also occur outside of Shelikof Strait.

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The incorporation of space into ecological models has increased our knowledge of the competition and co-existence among species (Steinberg and Kareiva, 1997). It has also shown that the distributions of most organisms are not homogeneous throughout their range, but rather occur as patches. Analyses of predator-prey interactions and food-web dynamics are enhanced by considering the habitat association of species. A first step towards this goal is to describe the spatial distributions of the major players in an ecosystem.

The purpose of our study was to examine changes in walleye pollock (*Theragra chalcogramma* (Pallas, 1814)) distribution. Walleye pollock (hereafter called "pollock") are a dominant species in the Gulf of Alaska (GOA). Pollock are the major prey of many species of flatfish and marine mammals and have been the predominant species in Steller sea lion (*Eumetopias jubatus* (Schreber, 1776)) diets since at least the mid-1970s (Pitcher, 1981; Merrick and Calkins, 1996). Numbers of Steller sea lions have declined significantly in recent decades in the western and central GOA. Examination of temporal and spatial changes in the abundance and population structure of pollock is important to understanding the decline in sea lion numbers. Existing and proposed management decisions to protect Steller sea lions include temporal and spatial changes to pollock fishing quotas.

The GOA pollock population peaked in the early 1980s as a result of several strong year classes in the late 1970s (Fig. 1A). Since then, the population has had fewer strong year classes. Modeled estimates of total biomass of the population declined in the early 1980s and leveled off in the 1990s (Fig. 1B). Bottom trawl survey biomass estimates (since 1984) have not reflected the decline in the early 1980s (Fig. 1C). Instead, they showed that the demersal fraction of the population changed little. Compared with other gadoid stocks worldwide, the GOA pollock stock has been lightly exploited; average landings have constituted less than 10% of the stock biomass during the last 20 years (Shima et al., 2000).

In this study we document changes in the spatial distribution and population density of juvenile and adult pol-

lock in the western and central GOA (defined as the area between 147°W and 170°W), from 1984 to 1996. Catch per unit of effort (CPUE) (number of fish/km^2) was used as a measure of density throughout our analysis.

We also examine changes in species associations and the distribution of pollock. Analysis is limited to the summer months because the source of our pollock data were summer research surveys.

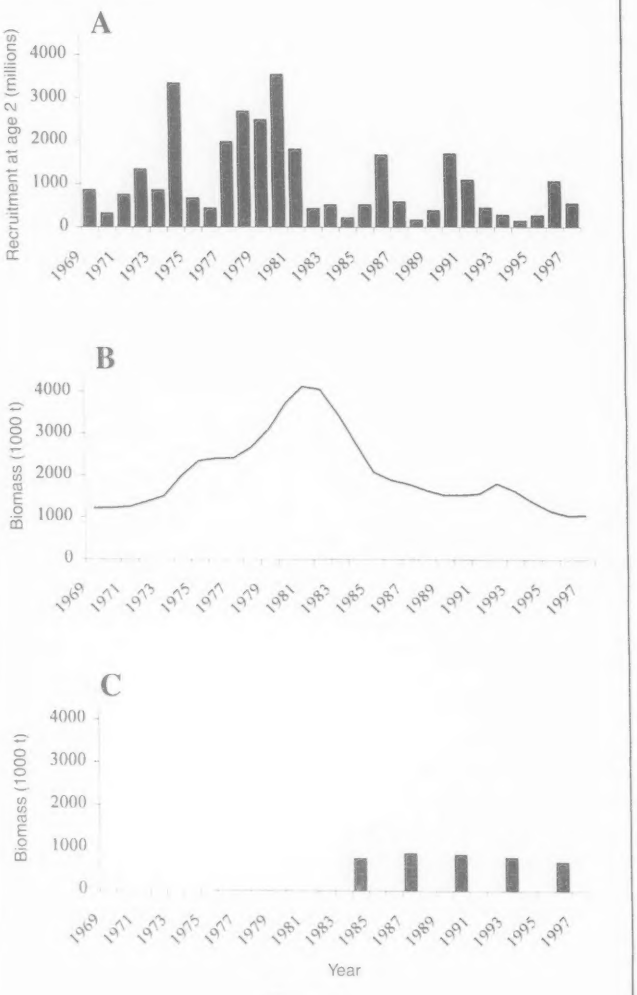

Figure 1

Data for walleye pollock in Gulf of Alaska, 1969–1997: pollock recruitment (**A**), biomass estimates from stock assessment analysis (**B**), and biomass estimates from triennial bottom trawl surveys (**C**). Data are from Dorn, M. W., A. B. Hollowed, E. Brown, B. Megrey, C. Wilson, and J. Blackburn. 2000. Walleye pollock. *In* Stock assessment and fishery evaluation report for the 2000 Gulf of Alaska groundfish fishery, 60 p. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, Alaska 99510.

Methods

Data source

Data were collected from triennial bottom trawl surveys in the GOA conducted by the Alaska Fisheries Science Center of the U.S. National Marine Fisheries Service (RACE division trawl survey relational database, Mundell[1]). The use of bottom trawl data to assess juvenile pollock abundance and distribution has many precedents. In the Bering Sea, bottom trawl survey data have been used to determine estimates of age-1 pollock, which were used as indices of recruitment (Wespestad[2]). Others have used the same data to evaluate the relationship between juvenile pollock and the movement of the ice edge in the Bering Sea (Wyllie-Echeverria and Wooster, 1998). Bottom trawl estimates have also been used to explore the relationships between different age groups of pollock in Shelikof Strait (Schumacher and Kendall, 1991).

Brodeur and Wilson (1996) modeled the depth distribution of pollock in the GOA during their first year and showed that age-1 pollock were found near bottom. Acoustic surveys of spawning pollock in Shelikof Strait have detected age-1 pollock in both nearbottom and pelagic layers. These data suggest that some age-1 pollock may reside off bottom. Therefore, juvenile pollock data from bottom trawl surveys are used as an index rather than an absolute measure of abundance (Bailey and Spring, 1992; Guttormsen and Wilson[3]).

Survey design

Triennial bottom trawl surveys were conducted during the summer months (May–Sep) of 1984, 1987, 1990, 1993, and 1996. These surveys have consistently been conducted in a stratified random sampling pattern (Martin and Clausen, 1995; Munro and Hoff, 1995; Stark and Clausen, 1995; Martin, 1997). The GOA is divided into 49 strata according to water depth

[1] Mundell, G. 1999. Personal commun. Alaska Fisheries Science Center, NMFS/NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

[2] Wespestad, V. 1995. Walleye pollock. *In* Plan team for groundfish fisheries of the Bering Sea/Aleutian Islands stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 1996, 35 p. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[3] Guttormsen, M. A., and C. D. Wilson. 1999. Echo integration-trawl survey results for walleye pollock in the Gulf of Alaska during 1998. *In* Stock assessment and fishery evaluation report for the 1998 Gulf of Alaska groundfish fishery, 25 p. North Pacific Fishery Management Council, 605 W 4th Avenue, Suite 306, Anchorage, Alaska 99501.

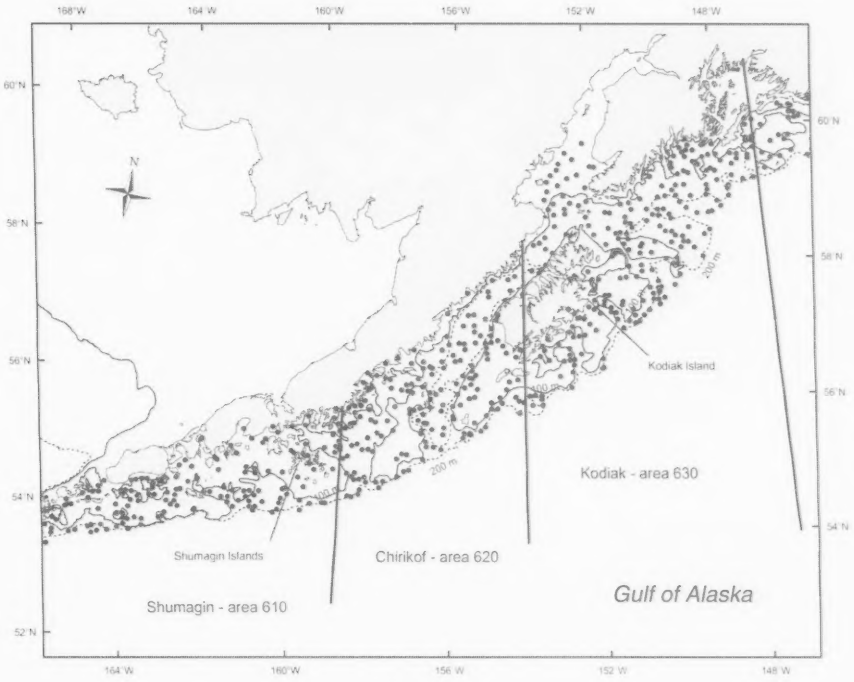

Figure 2

Example of the spatial coverage of the triennial bottom trawl survey for a sample year. Dots indicate station locations.

and area boundaries defined by the North Pacific Fisheries Management Council (http://www.fakr.noaa.gov/rr/figures/fig3.pdf). Allocation of sampling effort within each stratum was based on coefficients of variation, mean CPUE, and sampling densities for all fish species from data collected on previous triennial surveys (see Cochran, 1977). Sampling density within a stratum depended on the anticipated fish density of that particular stratum (Martin and Clausen, 1995; Stark and Clausen, 1995; Martin, 1997). Stations were prioritized within each stratum so that in the event of complications, sampling density would remain controlled. The total survey area was reduced by 7% after 1987 when stations deeper than 500 m were eliminated (Stark and Clausen, 1995). In the interest of consistency, only data from stations less than 500 m in bottom depth were used in our analyses. Station density was spread over a wide range; thus the survey data were most suitable for analyses of geographic distribution and community composition on a large scale (Fig. 2).

For each survey a Nor'eastern trawl (NT) with a 1.25 inch codend liner was used. The liner helped retain juvenile pollock (Brown, 1986). The nylon and polyethylene NTs had net dimensions of 18.3 m wide by 4.7 m high and 18.3 m by 5.5 m, respectively. In 1984 and 1987 a Japanese bottom trawl (JBT) was also used. The horizontal opening of the JBT ranged from 19 to 30 m, the vertical opening from 3.2 to 3.3 m (Brown, 1986). CPUE from the JBT were corrected (using Tables 28 and 31 in Munro and Hoff, 1995) to account for differences between the catchability of the NTs and the JBT.

Data analyses and statistical considerations

Analyses were conducted on total pollock catch as well as on four size groups of pollock: <150 mm (age-0 or young-of-the-year); 150–230 mm (age-1 juveniles); 230–330 mm (age-2 juveniles); and >330 mm (adults). The length-at-age categories were based on a histogram of pollock lengths from a historical database of all NMFS research surveys conducted during the summer. The catchability of age-0 pollock may not have been as high as that for the other juvenile age classes and thus supports the interpretation of all juvenile data as index values (Bailey and Spring, 1992; Guttormsen and Wilson, 1999). Comparable numbers of length measurements were taken every triennial year but measurements were not taken at every station. Thus, analyses of different age groups were based on subsets of the data. The abundance of fish in a specified age category was influenced by year-class strength (Table 1; Megrey et al., 1996; Hollowed et al.[4]). Strong year classes were present in 1984 (age 0), 1990 (age 2), and 1996 (age 2).

[4] Hollowed, A. B., E. Brown, B. Megrey, and C. Wilson. 1996. Walleye pollock. *In* Stock assessment and fishery evaluation report for the 1997 Gulf of Alaska groundfish fishery, 64 p. North Pacific Fishery Management Council, 605 W 4th A.venue, Suite 306, Anchorage, AK 99501.

Table 1
Summary of year-class strength of juvenile walleye pollock in bottom trawl survey years.

	1984	1987	1990	1993	1996
Age 0	Strong	Weak	Weak	Weak	Weak
Age 1	Weak	Weak	Average	Weak	Weak/Average
Age 2	Weak	Strong/Average	Strong	Weak	Strong

Marine surveys typically yield data sets that are highly variable and contain a substantial proportion of zero catches, particularly when the data set is broken down into age groups (Stefansson, 1996). Thus, in some cases the data were analyzed in terms of presence and absence of pollock (hereafter termed "occurrence"). Because nonzero data often follow a lognormal distribution (Pennington, 1996), the lognormal transformations (log(CPUE+1)) of nonzero density data were used during our analyses.

Changes in the depth distribution of pollock were analyzed by 100-m bottom depth intervals, corresponding to the depth stratification used in the triennial surveys. Changes in geographic distribution of CPUE were evaluated by GOA area boundaries, which again corresponded to the stratification design used during the triennial surveys. In our study, three areas were taken into consideration: "Shumagin" (159°–170°W, area 610), "Chirikof" (154°–159°W, area 620), and "Kodiak" (147°–154° W, area 630).

The distribution of pollock in relation to distance from land was evaluated in 20 nautical mile (nmi) increments by using GIS software (ESRI, Inc., 1996). However, the 20-nmi increments crossed the triennial survey strata boundaries, which may have resulted in the disruption of the stratified random sampling scheme. By addressing pollock occurrence or density at each station, instead of biomass, we avoided the need for stratifying the data after collection. Pollock usually reside at depths less than 300 m within the shelf and slope regions of the GOA (NPFMC[5]). Thus, the relatively narrow shelf region would limit the offshore distribution of pollock.

Initial exploratory analyses involved three-dimensional contingency tables to assess the relationship between the occurrence of pollock and year, bottom depth, geographic region, and distance from land. In cases where the three-dimensional analyses rejected the null hypothesis of independence, more detailed partial contingency tables were constructed for the occurrence of pollock against each individual variable. Other studies suggested that bottom depth and geographic location explain most of the variability in fish distribution data (e.g. Overholtz and Tyler, 1985; Jay, 1996).

[5] NPFMC (North Pacific Fishery Management Council). 1998. Essential fish habitat assessment report for the groundfish resources of the Gulf of Alaska region. NPFMC, 605 West 4th Avenue, Suite 306, Anchorage, AK 99501, 117 p.

Single-factor ANOVAs were performed on the nonzero CPUE data to examine the sources of variation in the data. The ln(CPUE+1) of the nonzero data was used as the dependent variable among years. A separate ANOVA was calculated for each category of bottom depth, geographic region, and distance from land.

Examination of the population density data revealed that for most age groups, the number of stations with a low density (<1000 fish/km^2) of pollock increased whereas the number of high-density stations remained relatively stable. This finding suggested that the distribution of suitable habitat for the demersal fraction of the population might have been expanding. Therefore, we examined the distribution of low-density concentrations of pollock separately in relation to the three physical characteristics across the survey years. Although ocean bottom temperature (OBT) was not measured at every survey station, available data were used to help interpret our results. Mean bottom temperature was averaged over bottom depth intervals for each year to provide a general overview (Fig. 3). Additional information on OBT has been summarized by S. Hare (http://www.iphc.washington.edu/staff/hare/html/papers/OBT/obt.html) from a variety of data sources and averaged over five-year periods.

Interspecies associations were examined with Bray-Curtis clustering techniques (Boesch, 1977; Walters and McPhail, 1982). Such classification techniques are useful in generating hypotheses about community structure, which may then be used to aid management actions (Cormack, 1971). Because the surveys used in the cluster analyses were conducted during the summer months, the results could not be extrapolated to other seasons. Triennial survey data were log-transformed and clustered by using the group average fusion strategy. For the species clusters, the top thirty species by weight were chosen in addition to the four age groups of pollock. After careful evaluation of all the cluster dendrograms, a common dissimilarity level (dissimilarity coefficient (h)=27) was chosen for all years as the level at which the most clearly defined clusters occurred throughout the triennial survey years.

Diversity indices were calculated for all five survey years. The top ten species by number of fish were combined for all years to make one list of species for which diversity was analyzed. Simpson's diversity index was calculated both in terms of richness and evenness (Simpson, 1949; Tokeshi, 1993). Richness was interpreted to mean "effective number of species," whereas evenness was un-

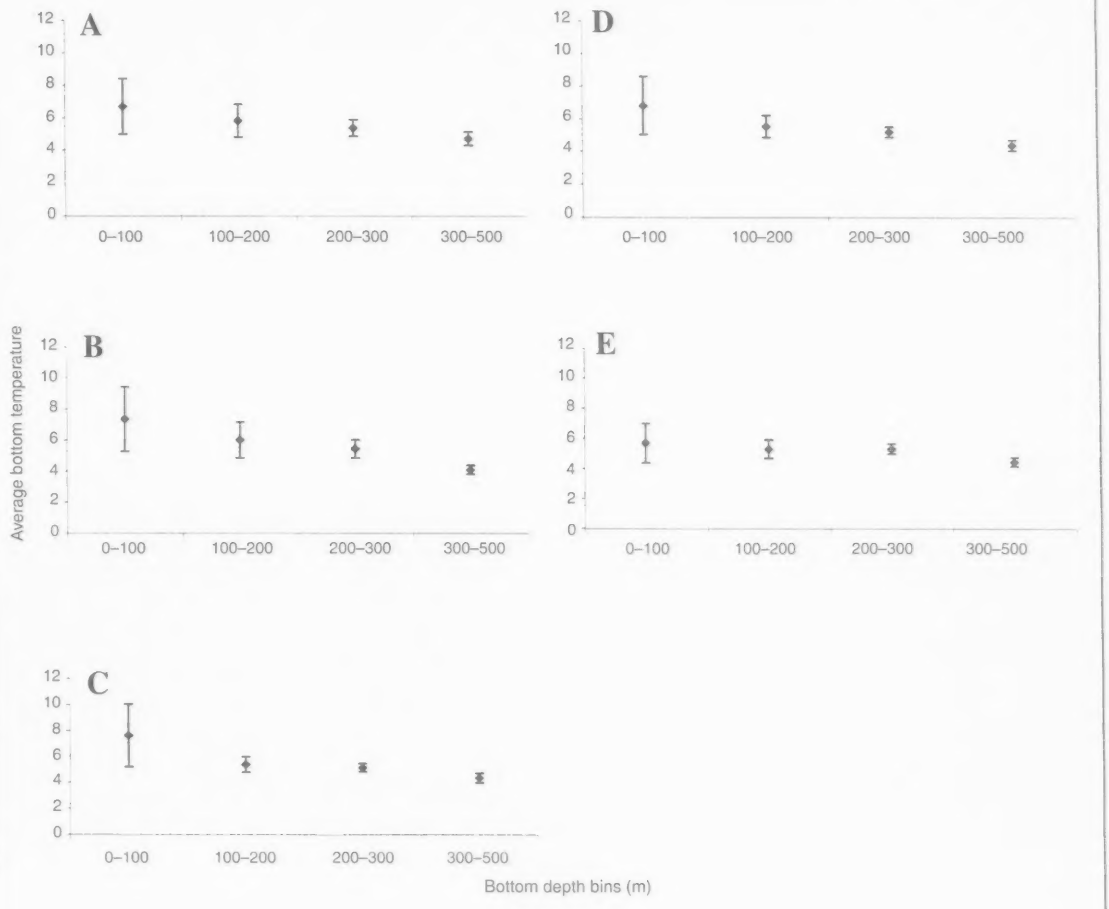

Figure 3

Average bottom temperature by bottom depth category from data collected during the triennial survey; (**A**) 1984, (**B**) 1987, (**C**) 1990, (**D**) 1993, (**E**) 1996. Error bars indicate 1 SD.

derstood to be the "distribution of numbers of fish amongst those species." Confidence intervals were calculated by jack-knifing the diversity index (Magurran, 1988).

Results

All pollock

Three-dimensional contingency tables indicated whether occurrence of pollock was mutually independent of all combinations of bottom depth, geographic region, distance from land, and year. The three-dimensional contingency tables for all three null hypotheses of mutual independence resulted in rejection of the null hypothesis ($P<0.001$). The null hypotheses considered for the three-dimensional and partial contingency tables are listed in Table 2. A summary of the distribution of stations within categories of the three physical characteristics is given in Table 3. All the hypotheses of partial independence on combinations of two of the physical characteristics could be rejected ($P< 0.001$). When each physical characteristic was tested separately, the only hypothesis that could not be rejected ($\alpha=0.05$) was the independence of pollock occurrence against geographic region ($P=0.097$, Table 2). Graphs of pollock occurrence versus each of the physical characteristics revealed distinctive patterns (Fig. 4). The graphs indicated that pollock are most frequently observed in the 100–200 m bottom depth interval and the 0–20 nmi distance category (Fig. 4, A and B). However, this interpretation may be an artifact of the percentage of stations sampled within each category (Table 3). For all years, the

greatest number of stations were sampled in the 100–200 m bottom-depth category and in the 0–20 nmi distance–from-land category.

The results were standardized by taking the proportion of stations within each category that had a positive occurrence of pollock (Fig. 5). These graphs showed that for each bottom depth category, the proportion of positive occurrences had increased over the years. The proportion of stations where pollock were present was consistently high in the 0–20 nmi category (Fig. 5). Farther from land, the proportion of positive stations increased between 1984 and 1996. In all three geographic regions, there was an increase in the proportion of stations where pollock were present.

Table 4 lists the number of hauls with pollock occurrence and summarizes the CPUE values for the nonzero data. Results from the single-factor ANOVAs calculated for the nonzero density data are summarized in Table 5. Significant differences were observed among most years, except for the Chirikof region and the distances from land of 0–20 and 40–60 nmi.

Table 2

Contingency table analysis of walleye pollock occurrence.

Type of table	*P*-value
Three-dimensional tables of mutual independence	
Null hypothesis	
Pollock occurrence, year, and bottom depth are mutually independent	$P< 0.001$
Pollock occurrence, year, and distance from land are mutually independent	$P< 0.001$
Pollock occurrence, bottom depth, and region are mutually independent	$P< 0.001$
Pollock occurrence, region, and distance from land are mutually independent	$P< 0.001$
Three-dimensional tables of partial independence	
Null hypothesis	
Pollock occurrence is independent of year and bottom depth	$P< 0.001$
Pollock occurrence is independent of year and distance from land	$P< 0.001$
Pollock occurrence is independent of bottom depth and region	$P< 0.001$
Pollock occurrence is independent of region and distance from land	$P< 0.001$
Two-dimensional tables of partial independence	
Null hypothesis	
Pollock occurrence is independent of year	$P< 0.001$
Pollock occurrence is independent of bottom depth	$P< 0.001$
Pollock occurrence is independent of region	$P=0.097$
Pollock occurrence is independent of distance from land	$P< 0.001$

Adult pollock

The initial three-dimensional contingency tables of mutual independence between adult pollock occurrence and the three physical characteristics proved significant. Subsequent contingency analyses revealed significant results for all partial independence tests except for the two-dimensional test for independence between occurrence of adult pollock and geographic region (P=0.58).

Examination of all the positive data showed that the mean of the log-transformed CPUE decreased and the variance increased over time for bottom depths 100–200 m in each geographic area (Table 6). The mean CPUE also decreased over time for stations <40 nmi from land but there was no trend in the changes in variance (Table 6). The ANOVA confirmed that changes in the distribution of pollock from 1984 to 1996 were significant (α=0.05) among years at all depth intervals, all geographic areas , and at a distance from land <60 nmi (Table 7). Thus, although the number of stations where pollock could be encountered increased (e.g. the low-density distribution data), the mean adult pollock density decreased and became more variable between 1984 and 1996 (Fig. 5, Table 6).

Changes in the distribution of adult pollock were further examined by sorting the data into seven CPUE bins and by making histograms of the frequency of stations within each bin (Fig. 6). The histogram revealed that over the years, the occurrence of stations with zero adult pollock CPUE decreased, whereas stations with low-density (CPUE <1000 fish/km^2) concentrations of pollock increased. Higher density stations did not exhibit any particular trend.

To better understand observed changes in the distribution of low-density concentrations of adult pollock, all the stations were characterized by bottom depth, geographic location, and distance from land (Fig. 7). The number of stations that had low-density concentrations of adult pollock increased in all habitat categories over the years. The proportion of stations within each bottom depth bin with low-density concentrations of adult pollock more than doubled from 1990 to 1996. Comparable dramatic increases were observed with regard to distance from land and geographic region.

Juvenile pollock

Contingency table analysis for juvenile pollock occurrence resulted in significant (P<0.001) results across all ages for tests of mutual independence among all the physical characteristics. Two-dimensional contingency analyses also resulted in significant results. It was difficult to discern any chronological trends in the mean and variance of all the positive data for juvenile pollock. Minor fluctuations in juvenile pollock density may have been related to interannual differences in year-class strength (Table 1).

Histograms similar to those for adult pollock were made for all three juvenile age groups of pollock, where juvenile

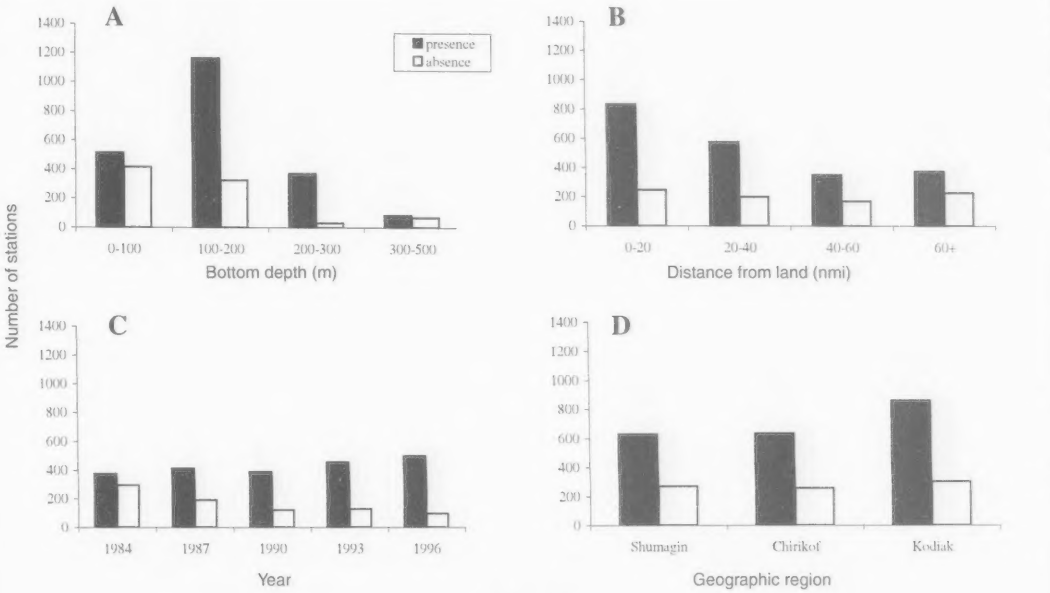

Figure 4

The number of stations at which walleye pollock occurred by physical characteristic: (**A**) bottom depth (m); (**B**) distance from land (nmi); (**C**) year; and (**D**) geographic region.

Table 3

Summary of the percentage of stations within each bin for the three types of physical parameters discussed in the text. The number in parentheses indicates the total number of stations.

	Percentage of stations in category by year				
Physical category	1984 (749)	1987 (648)	1990 (534)	1993 (616)	1996 (613)
Bottom depth (m)					
0–100	29.9	33.7	23.7	32.8	35.4
100–200	46.1	53.7	59.1	50.9	43.2
200–300	16.5	9.6	13.8	12.0	14.7
300–500	7.4	3.0	3.4	4.3	6.7
Geographic location					
Shumagin	33.2	28.5	26.7	29.3	33.7
Chirikof	27.5	32.5	30.8	29.5	30.9
Kodiak	39.3	40.0	42.5	41.2	35.4
Distance from land category (nmi)					
0–20	28.9	39.3	36.2	38.1	40.6
20–40	27.2	25.7	25.5	27.4	23.9
40–60	19.2	16.9	20.4	16.6	14.3
60+	24.7	18.1	17.9	17.8	21.1

pollock density was parsed into bins and plotted (Fig. 8). The same trend seen in the adults was also seen with the juvenile pollock. As the years progressed, there was an increase in the proportion of stations that had low-density (<1000 fish/km^2) concentrations of all juvenile age groups of pollock. For age-0 and age-1 pollock, there was about a tenfold difference in the proportion of stations with low-density concentrations after 1987 (Fig. 8). Age-2 pollock

Table 4

Summary information of walleye pollock occurrence and CPUE by triennial survey year. CPUE values are given in number of fish/km^2 and summarize only the nonzero positive tows.

	Number of hauls		CPUE			
Year	Total	Pollock present	Minimum	Maximum	Mean	SD
1984	672	375	11.48	397079.10	9759.45	31564.10
1987	603	412	13.85	602901.72	9640.16	43282.89
1990	506	386	16.77	130009.85	6866.74	15946.86
1993	583	454	19.03	218130.41	4994.91	15947.79
1996	593	497	32.22	239402.07	5434.23	18829.21

Table 5

Single-factor ANOVAs of ln(CPUE+1) of positive walleye pollock catches among years by bottom depth category, geographic region, and distance from land. SS = sum of squares; MS = mean square.

	SS	df	MS	*F*	*P*
Bottom depth (m)					
0–100	73.60	4	18.40	3.37	0.01
100–200	91.04	4	22.76	4.24	<0.001
200–300	77.22	4	19.31	6.47	<0.001
300–500	19.00	4	4.75	3.19	0.02
Geographic area					
Shumagin	84.68	4	21.17	3.94	<0.001
Chirikof	24.29	4	6.07	1.16	0.33
Kodiak	185.06	4	46.27	10.47	<0.001
Distance offshore (nmi)					
0–20	23.80	4	5.95	1.21	0.30
20–40	71.94	4	17.99	3.51	0.01
40–60	29.94	4	7.49	1.66	0.16
60+	56.66	4	14.17	3.99	<0.001

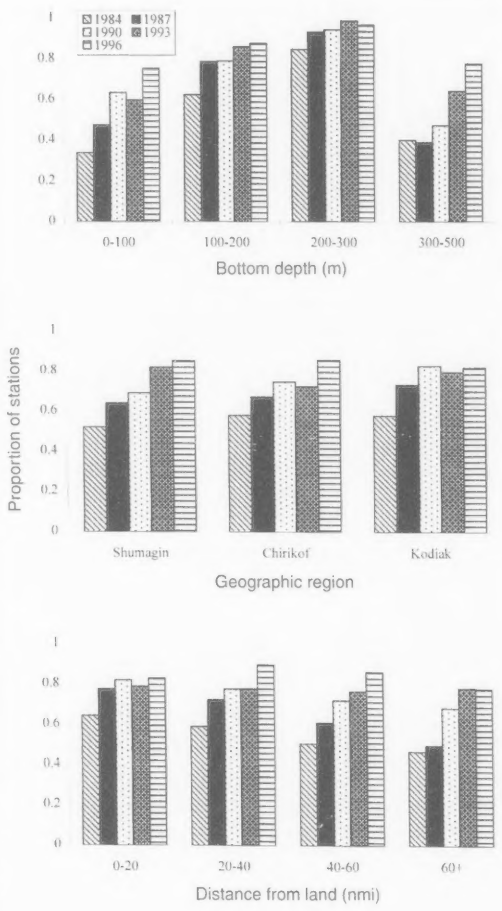

Figure 5

The proportion of stations within each category of physical characteristic where walleye pollock were found .

also exhibited this trend but not to the same degree as age-0 and age-1 pollock.

Stations with low-density concentrations of juvenile pollock were examined with respect to bottom depth, geographic area, and distance from land (Fig. 9). For all ages of juvenile pollock there was a marked difference between 1984–87 and the 1990s. A greater proportion of stations with age-0 pollock was observed at bottom depths <200 m than at deeper depths, especially in 1996. Age-0 pollock occurrence increased in the Chirikof and Shumagin regions before also increasing in the Kodiak region in 1996. Age-0 pollock also occurred more frequently at distances <60 nmi from land.

In 1990, the proportion of stations with low-density concentrations of age-1 pollock increased the most at bottom depths >200 m, before the same increasing trend was also observed at shallower bottom depths in 1993 and 1996 (Fig. 9). The increase was observed across all geographic regions and at all distances from land.

Table 6

Mean and variance estimates of ln(CPUE+1) for 1984–96 for nonzero adult pollock data by physical characteristic. The number of observations is given in parentheses.

	Mean					Variance				
Physical characteristic	1984	1987	1990	1993	1996	1984	1987	1990	1993	1996
Bottom depth (m)										
0–100	8.05 (24)	8.59 (37)	7.05 (23)	6.73 (74)	6.41 (108)	3.45	2.80	3.87	7.71	5.38
100–200	8.84 (121)	8.66 (110)	8.17 (158)	6.74 (204)	6.20 (192)	2.77	2.43	2.56	3.81	4.23
200–300	7.82 (52)	8.14 (24)	7.68 (60)	6.58 (64)	5.88 (82)	2.40	0.70	1.59	1.68	1.69
300–500	7.02 (1)	0 (1)	7.43 (1)	5.28 (12)	4.70 (30)	0	0	0	0.30	0.88
Geographic area										
Shumagin	8.80 (63)	8.45 (37)	7.40 (33)	6.63 (101)	6.32 (121)	2.65	2.35	2.30	5.54	3.72
Chirikof	8.09 (57)	8.62 (49)	7.91 (52)	6.65 (83)	5.74 (125)	3.64	2.47	2.65	3.23	3.71
Kodiak	8.47 (78)	8.62 (82)	8.22 (134)	6.91 (138)	6.42 (138)	2.53	2.23	2.50	3.94	4.21
Distance from land (nmi)										
0–20	8.49 (141)	8.67 (140)	8.04 (161)	7.02 (236)	6.40 (269)	2.90	2.15	2.76	4.42	4.28
20–40	8.50 (42)	7.76 (19)	7.59 (57)	5.79 (96)	6.12 (86)	3.57	2.33	1.93	2.75	1.36
40–60	8.16 (13)	8.66 (10)	5.31 (16)	6.23 (20)	8.00 (40)	1.88	3.46	2.20	2.52	2.24
60+	5.38 (2)	5.95 (2)	8.26 (8)	6.66 (10)	5.66 (7)	4.54	4.55	2.53	4.42	2.55

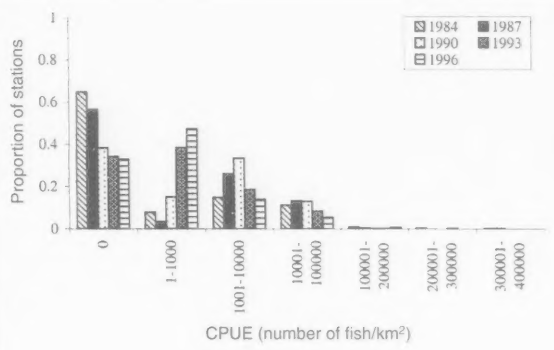

Figure 6

Porportion of stations for different density levels of adult walleye pollock.

Table 7

Single-factor ANOVAs of ln(CPUE+1) of positive adult walleye pollock catches among years by bottom depth category, geographic region, and distance from land. SS = sum of squares; MS = mean square.

	SS	df	MS	*F*	*P*
Bottom depth (m)					
0–100	162.23	4	40.56	7.55	<0.001
100–200	872.70	4	218.17	65.99	<0.001
200–300	196.38	4	49.09	30.76	<0.001
300–500	37.80	4	9.45	13.04	<0.001
Geographic area					
Shumagin	345.66	4	86.42	22.87	<0.001
Chirikof	448.03	4	112.01	34.19	<0.001
Kodiak	453.24	4	113.31	35.09	<0.001
Distance (nmi)					
0–20	758.52	4	189.63	53.61	<0.001
20–40	417.66	4	104.41	40.42	<0.001
40–60	174.97	4	43.74	18.59	<0.001
60+	30.82	4	7.70	2.48	0.071

There was a general increase over time of low-density concentrations of age-2 pollock with respect to bottom depth and geographic region (Fig. 9). The increase in the proportion of low-density concentrations of age-2 pollock was the greatest 20–60 nmi from land until 1996, when the proportion of stations with low-density concentrations increased the most >60 nmi from land.

Community composition

Results of clustering by species by using the triennial bottom trawl data are presented in Table 8. The top 30 species or species types (e.g. adult and juvenile pollock) by weight over all survey years were chosen. Adult pollock were consistently associated over the years most closely with flathead sole (Table 8). The cluster containing adult pollock usually included 3–6 other species of importance, either commercially or in terms of abundance. These included arrowtooth flounder (*Atheresthes stomias* (Jordan

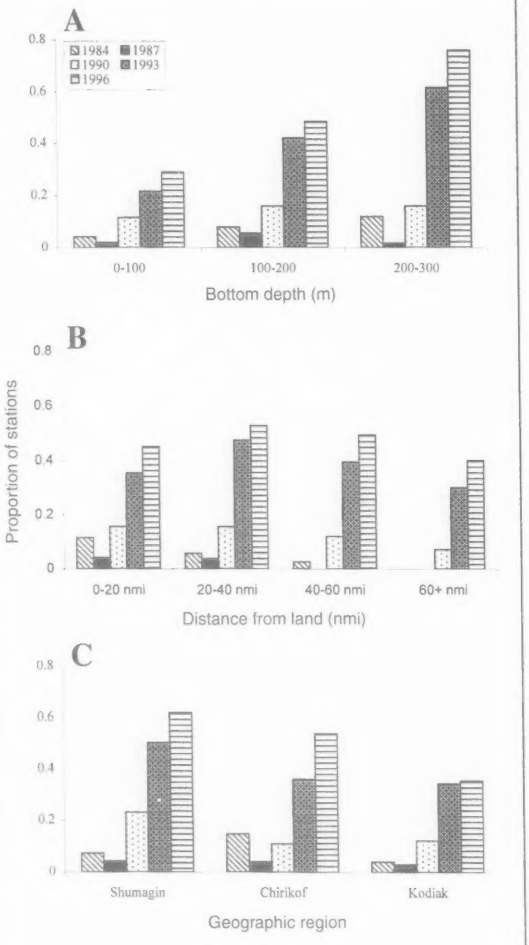

Figure 7

Proportion of stations where low-density concentrations (<1000 fish/km^2) of adult walleye pollock were observed, binned by bottom depth (**A**), distance from land (**B**), and geographic region (**C**).

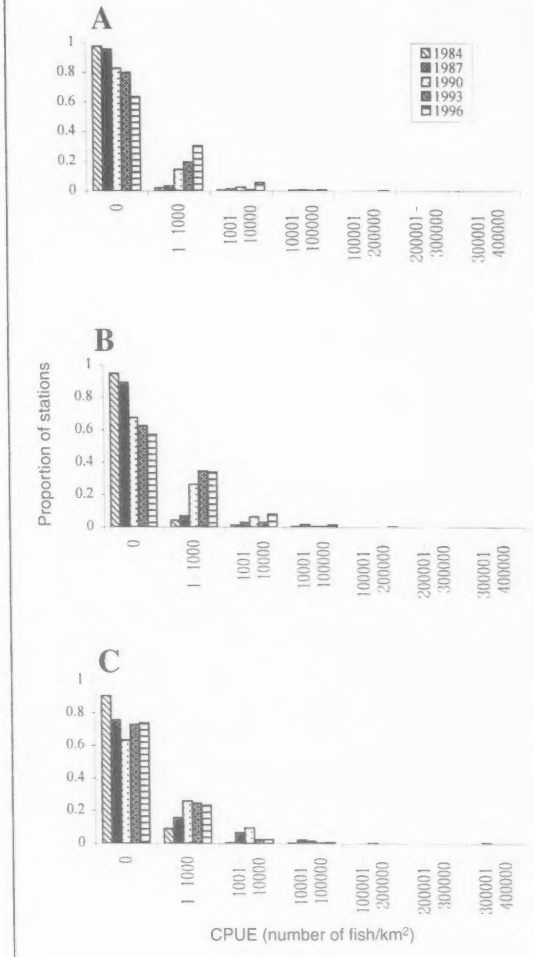

Figure 8

Proportion of stations with different levels of juvenile walleye pollock CPUE; age 0 (**A**), age 1 (**B**), and age 2 (**C**).

and Gilbert, 1880)), Pacific halibut (*Hippoglossus stenolepis* Schmidt, 1904), Pacific cod (*Gadus macrocephalus* Tilesius, 1810), sablefish (*Anoplopoma fimbria* (Pallas, 1814)), Dover sole (*Microstomus pacificus* (Lockington, 1879)), and rex sole (*Glyptocephalus zachirus* Lockington, 1879). This small cluster was usually isolated from the larger main cluster (i.e. high dissimilarity between the two clusters). Adult pollock were also clustered separately from the juvenile pollock age groups. In all years except 1987, age-1 and age-2 pollock were clustered with each other, whereas age-0 pollock were clustered separately. In 1987, age-0 and age-1 pollock clustered together, although not as closely associated as ages 1 and 2 in the other years. Until 1996, age-0 pollock clustered with Pacific sleeper shark (*Somniosus pacificus* Bigelow and Schroeder, 1944), Aleutian skate (*Bathyraja aleutica* (Gilbert, 1896)), or silvergray rockfish (*Sebastes brevispinis* (Bean, 1884)). In the larger cluster that contained all the juvenile pollock age groups, it was common to find Pacific herring (*Clupea pallasii* (Cuvier and Valenciennes, 1847)) in all years.

Cluster analysis by station of the triennial data resulted in clusters that fell into clean zoogeographic groups that followed depth contours. Maps of clusters identified seven groups of species that could be tracked in the GOA throughout most years (Table 9). Groups 1, 2, and 5 were present only in 4 out of the 5 triennial survey years. In 1984, groups 2 and 5 were absent whereas in 1990, group 1 was absent. The species within each cluster were listed in order of dominance. Although many of the clusters had

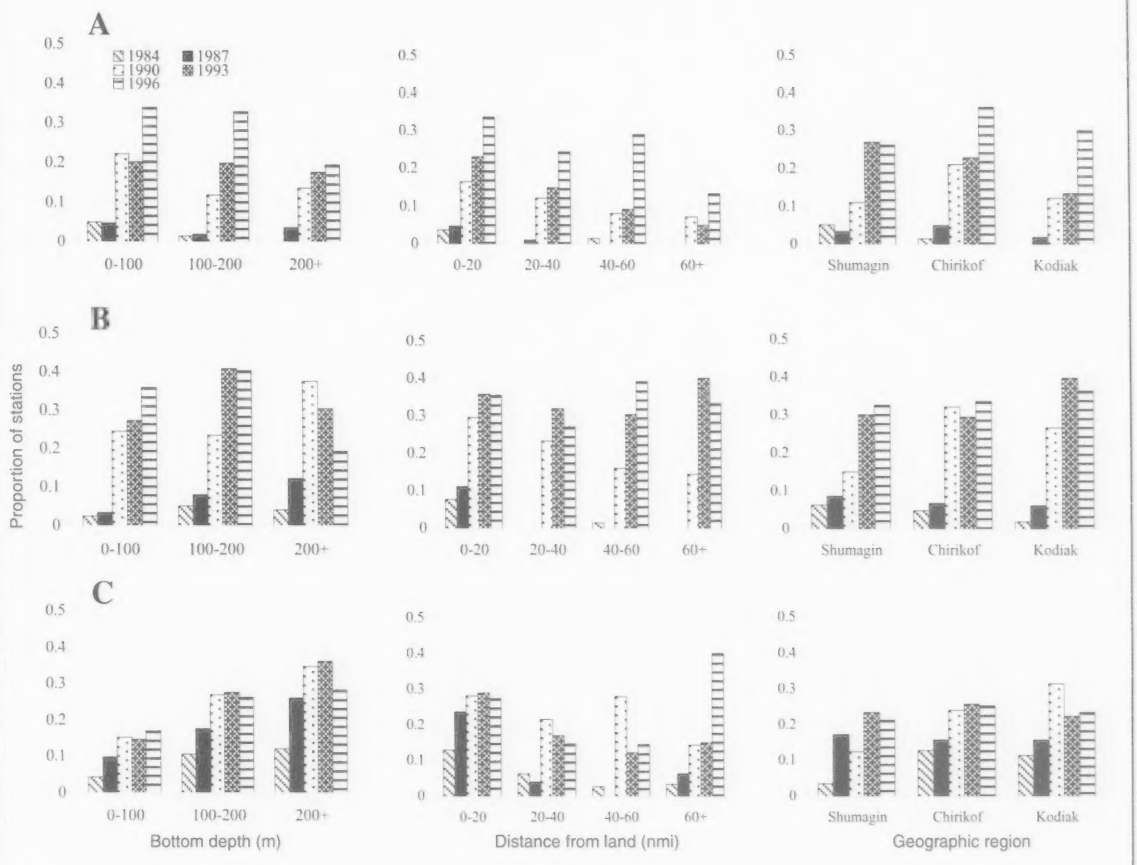

Figure 9

Proportion of stations with low-density concentrations (<1000 fish/km^2) of juvenile pollock by bottom depth (first column), distance from land (second column), and geographic region (third column) for age 0 (**A**), age 1 (**B**), and age 2 (**C**) juveniles.

the same main species in common, as listed in Table 9, differences in dominance distinguished the various clusters. Adult pollock were most dominant in groups 1, 3, and 6, which were either made up of nearshore or deep shelf stations (Table 9). Mean values of several environmental variables in these station groups in which pollock were found indicate that bottom depth and temperature varied (Table 9). Shallow water stations (groups 1 and 2) were grouped into warm (6.4°C) and average (5.7°C) bottom temperature clusters (Table 9). As expected, deeper water stations tended to be characterized by cooler temperatures. Juvenile (ages 0–2) pollock were found mostly in the nearshore stations.

Diversity

Separate diversity indices were calculated for habitat between 0–100 m bottom depth and 100–200 m bottom depth. In the 0–100 m habitat, there was a slight decrease in richness from 9–10 in the 1980s to 7–9 effective number of species in the 1990s (Fig. 10A). Calculations of evenness for the same data indicated that there had been little change in the evenness component of species diversity in the 0–100 m habitat (Fig. 10C). Histograms of the proportion (in terms of number of fish) contributed by each of the top species indicated that the decrease in richness might partially be explained by an increase in the predominance of pollock and a decrease in the presence of rockfish species (Fig. 11, A–E).

Richness in the 100–200 m category increased from 5 to 10 effective numbers of species (Fig. 10B). The predominance of pollock and arrowtooth flounder in the 1980s had shifted to include eulachon (*Thaleichthys pacificus* (Girard, 1858)) and Pacific ocean perch (*Sebastes alutus* (Gilbert, 1890); Fig. 11, F–J). Evenness was relatively consistent throughout the survey years (Fig. 10D).

Discussion

A major result of our study was that for all age groups of pollock, the number of stations where pollock occurred at low densities (<1000 fish/km^2) increased during 1984–96 while the mean density decreased. This pattern suggests that the pollock population was increasing its range, a characteristic often seen in growing populations that is consistent with the "basin hypothesis" (MacCall, 1990). MacCall hypothesized that at low-densities, marine fish will occupy habitats that are optimal for survival. As populations grow, however, some portions of the populations will expand into locations of less suitable habitat quality.

Our analyses of the data indicated that the demersal portion of the pollock population was stable but that the overall (pelagic and demersal) pollock population declined during the study (1984–96, Fig. 1, B and C). Year-class strength was only sporadically strong and therefore would not account for the sustained increased positive occurrence by station during the early- to mid-1990s. Under MacCall's hypothesis, the range of the population should have been stable or contracting. Thus, patterns emerging from our data are not entirely consistent with MacCall's model.

Analysis of CPUE of all positive tows revealed that there was a decrease in mean CPUE over the years from 1984 to 1996. The data showed an increase in low-density concentrations of adult pollock stations across all categories but in particular at bottom depths 200–300 m and in the Chirikof and Shumagin regions. We conclude that adult pollock had expanded into deeper water in the 1990s but that the expansion had resulted in a decrease of adult pollock in high-density stations, combined with decreased mean density of adult pollock throughout the region. We hypothesize that the expansion of pollock was due to an increase in the suitability of habitats for adult pollock, possibly caused by a spread in the distribution of pollock forage, during a period of stable or decreasing pollock population trends. If predators of pollock rely on high-density patches, the decreased mean density of pollock may have negative ramifications for the successful foraging of top predators. We refer to this as the "forage density hypothesis"; i.e. habitat suitability has changed, perhaps on a local scale, such that there has been an expansion of the overall population distribution. However, the expansion, combined with decreasing population numbers, had caused the density of pollock patches to decrease below a threshold at which top predators can successfully forage. The underlying assumption here is that the predators need patches of high prey density rather than a uniform distribution of average or low prey density.

Analysis of trends in the distribution and abundance of juvenile age groups is more difficult because data for

Table 8

Species associated with walleye pollock according to Bray-Curtis cluster analyses of triennial survey data. The species are listed in order of association.

Adults	Age 0	Ages 1 and 2
Flathead sole	Pacific sleeper shark	Atka mackerel
Sablefish	silvergray rockfish	eulachon
Dover sole	lingcod	Pacific herring
Rex sole	longnose skate	bigmouth sculpin
Arrowtooth flounder	sharpchin rockfish	lingcod
Pacific halibut	Pacific herring	chinook salmon
Pacific cod		

Table 9

Description of consistent station groups found as a result of cluster analyses of the triennial bottom trawl survey data. The group designation "flatfish" includes all flatfish except arrowtooth flounder. Mean values are given for the environmental variables. Standard deviations are given in parentheses.

Group no.	Location	Bottom depth (m)	SST (°C)	Temperature at depth (°C)	Main species
1	Nearshore 1	85.9 (32.1)	9.7 (2.4)	5.7 (4.9)	Age 2 and Adult pollock, Flatfish
2	Nearshore 2	83.7 (38.4)	9.4 (2.4)	6.4 (1.7)	Adult pollock, Flatfish, Pacific cod
3	Shallow shelf	119.9 (47.7)	9.0 (2.5)	5.8 (1.9)	Arrowtooth flounder, Adult pollock, Pacific halibut, Pacific cod
4	Deep shelf	120.6 (31.9)	9.5 (2.2)	5.5 (0.7)	Arrowtooth flounder, Flatfish, Pacific cod, Adult pollock
5	Inner slope	167.0 (50.3)	10.9 (2.2)	5.6 (0.8)	Northern rockfish, Pacific ocean perch, Arrowtooth flounder
6	Middle slope	197.1 (80.4)	10.1 (2.9)	5.3 (0.7)	Adult pollock, Pacific ocean perch, Arrowtooth flounder, Sablefish
7	Outer slope	412.9 (153.5)	10.7 (3.1)	4.9 (0.9)	Giant grenadier, Sablefish, Rockfish

these age groups are strongly influenced by interannual variations in year-class strength. However, spatial trends in distribution were consistent with those seen for adult pollock. For all age groups of juvenile pollock there was an increase in the proportion of stations where low densities occurred, and a decrease in the mean CPUE during the time period examined.

The spatial expansion by a species should be reconciled with more detailed analyses of the characteristics of the area it occupied to determine whether changes in habitat suitability have occurred. Adult pollock are not expanding into areas with physical characteristics previously not associated with pollock. Cluster analysis revealed that adult pollock are associated with average bottom temperatures between 5.2°C and 6.4°C. The bottom temperature data from field surveys revealed a consistent range over time of 5–6°C (Dorn et al.[6]). It was difficult to discern a trend from either our bottom temperature or the OBT data. Temperatures may have been slightly warmer in the 1980s than in the 1990s. Temperature changes, together with the shoaling of the mixed layer depth (Polovina et al., 1995; Shima, 1996), may have caused a redistribution of prey, possibly contributing to changes in pollock distribution.

Evidence of the importance of external forcing on the spatial range of fish species has been noted in other ecosystems. Movement of fish in response to environmental change was recorded in the Barents Sea when Atlantic cod (*Gadus morhua* Linnaeus, 1758) shifted westward as a consequence of cooler waters (entering from the east) across the region from 1977–81 (Loeng, 1989). Primary shifts in distribution, in response to temperature changes, were seen in younger age classes of fish. Because there were some species (e.g. haddock, *Melanogrammus aeglefinus* (Linnaeus, 1758)) that did not respond to changes in temperature, it may be that the movement of the fish may be dependent on the sensitivity of fish prey to the temperature shifts (Shevelev et al., 1987). Cod (like pollock) feed mostly on planktonic organisms that may respond rapidly to temperature changes whereas haddock feed mostly on benthic species (Shevelev et al., 1987).

External forcing may also include anthropogenic factors. Domestication (U.S.) of the pollock fishery occurred during the period investigated (Megrey, 1989) with the result that fishing operations shifted from at-sea processors

[6] Dorn, M. W., A. B. Hollowed, E. Brown, B. Megrey, C. Wilson, and J. Blackburn. 1999. Walleye pollock. *In* Stock assessment and fishery evaluation report for the 2000 Gulf of Alaska groundfish fishery, 65 p. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, Alaska 99510.

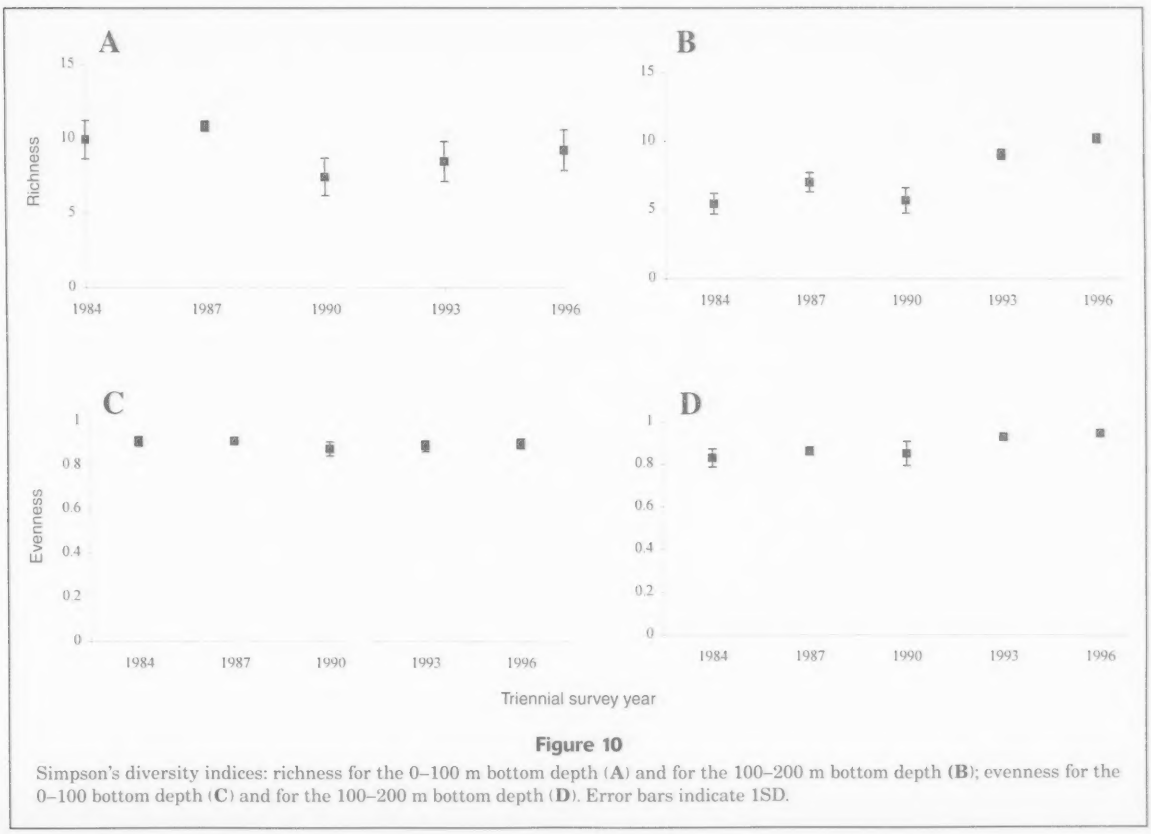

Figure 10

Simpson's diversity indices: richness for the 0–100 m bottom depth (**A**) and for the 100–200 m bottom depth (**B**); evenness for the 0–100 bottom depth (**C**) and for the 100–200 m bottom depth (**D**). Error bars indicate 1SD.

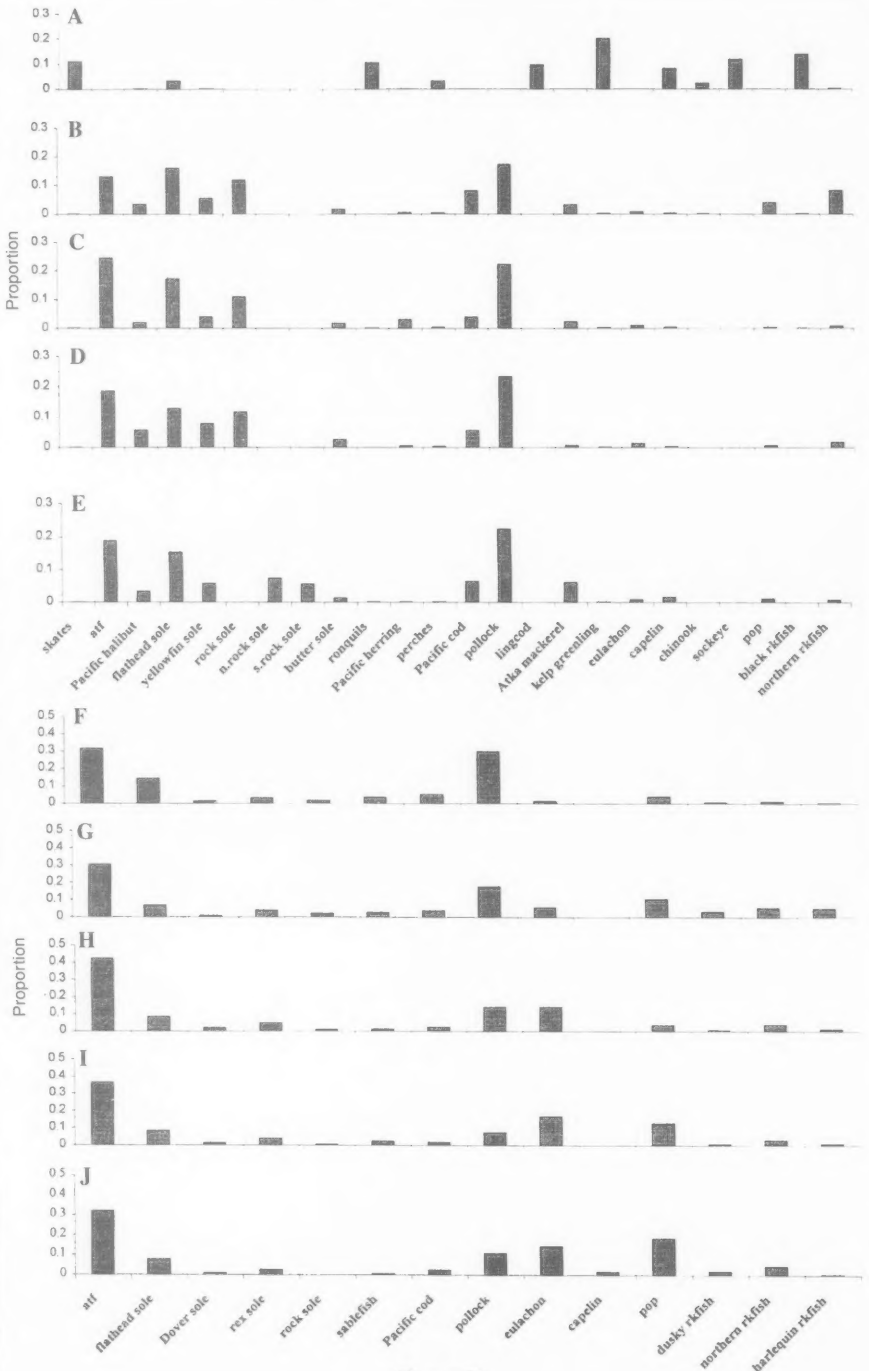

Figure 11

Proportion of the top species included in the diversity index calculations for 1984–96 in the 0–100 m bottom depth interval (**A–E**) and the 100–200 m bottom depth interval (**F–J**). Some fish species names have been abbreviated: atf = arrowtooth flounder, n. rock sole = northern rock sole, s. rock sole = southern rock sole, pop = Pacific ocean perch, rkfish = rockfish.

to a reliance on shoreside processing. The shift moved fishing operations closer to shore after the mid-1980s (Fritz[7]). Studies in other regions have found that groundfish species (Pacific whiting and haddock) disperse as a result of trawling. However, within minutes of a vessel's passage, the fish usually revert back to their original distribution (Ona and Godøø, 1990; Nunnallee[8]). It should be noted that this behavior is the result of disturbance by a single vessel. It is possible that the activity of multiple vessels that make up commercial fisheries could cause long-term redistribution of pollock. Studies are currently underway to examine the potential effect of commercial fisheries on the distribution of pollock (Hollowed et al.[9]).

Predator-prey interactions also influence the distribution of marine fish. Adult pollock are capable of exhibiting a strong top-down influence on juvenile abundance through cannibalism (Livingston, 1991). However, in the GOA the incidence of cannibalism is minimal (Yang, 1993), perhaps because, as shown in our study, the ranges of adult and juvenile pollock do not overlap. Spatial distributions showed that the bulk of both adult and juvenile pollock occurred in the Kodiak and Chirikof regions in the GOA. Mean density for both juveniles and adults was high within 20 nmi from land. However, age-0 (and often age-1) pollock were in greatest density in shallow waters <20 nmi from land, whereas adult pollock tended to occupy deeper waters. Age-2 pollock, which are beyond the size range that adult pollock target as food in the Bering Sea, tend to have a distribution similar to that of adults. The separation between juveniles and adults could be a seasonal effect due to the summer sampling season of the surveys because juvenile pollock are known to migrate ontogenetically (Brodeur and Wilson, 1996). However, the pattern of spatial separation between age-0 and age-1 pollock and adult pollock may indicate avoidance of adults by juvenile pollock.

An examination of changes in density of juvenile pollock in relation to geographic location allowed evaluation of the prevailing conceptual model for pollock ontogeny in the Gulf of Alaska (Kendall et al., 1996). The majority of spawning for the GOA stock occurs in the Shelikof Strait region (Kendall and Picquelle, 1989; Hinckley et al., 1991; Kendall et al., 1996). Survey and ocean modeling studies show that larvae and early juveniles are advected by the Alaska Current towards the Shumagin Islands (Hinckley et al., 1991; Hermann et al., 1996; Hinckley, 1999). Our results are partially consistent with the conceptual model for pollock ontogeny: the area encompassing Shelikof Strait and west to the Shumagin Islands (i.e. the Kodiak and Chirikof regions) was important for all juvenile age groups. However, the disproportionate increase of pollock in the Kodiak region in the 1990s, with two strong year classes (1988 and 1994), supports the suggestion that substantial spawning may also occur outside of Shelikof Strait (Smith et al., 1984; Brodeur and Wilson, 1996).

The species composition of the cluster in which pollock was included changed little over the course of the survey years. Adult pollock were usually located together with commercially important flatfish, arrowtooth flounder, and Pacific cod. This finding is consistent with other findings from the eastern Bering Sea where pollock often were associated with snow and Tanner crabs (*Chionoecetes* spp.), Pacific cod, flathead sole, Greenland turbot (*Reinhardtius hippoglossoides* (Gill, 1861)), and yellowfin sole (*Limanda aspera* (Pallas, 1814)) from 1978 to 1981 (Walters and McPhail, 1982).

Depth contours served as demarcations of station clusters in our study as well as in others conducted in the eastern Bering Sea and the eastern Pacific Ocean along the western coast of the United States (Gabriel and Tyler, 1980; Walters and McPhail, 1982; Jay, 1996). The consistency in how the stations were grouped together is common throughout all these studies. Walleye pollock in the eastern Bering Sea also dominated clusters of stations in the central shelf or the outer shelf. Other species commonly found together with pollock in these groups were yellowfin sole and Pacific cod.

A hypothesis relating pollock distribution to sea lion foraging behavior

Because pollock predominate the Steller sea lion diet (Merrick and Calkins, 1996), the temporal and spatial changes in pollock abundance and distribution could affect Steller sea lions. The Steller sea lion population underwent precipitous declines in the 1980s and declines continued in the 1990s but not as steep (Sease et al., 1999; NMFS[10]). The rate of decline continues to be high towards the center of the Gulf of Alaska (150–158°W), whereas the western Gulf region (158–162°W) has stabilized (i.e. the rate of decline has decreased).

Survey results suggest that the "forage density hypothesis" may apply to Steller sea lions in the GOA. There is evidence indicating that Steller sea lions target dense aggregations of prey (Sinclair and Zeppelin, in press), so that the lower mean density of pollock may reduce the number of successful Steller sea lion foraging trips in the central GOA. This effect may have prevented the sea lion population from recovering from the precipitous decline that oc-

[7] Fritz, L. W. 1993. Trawl locations of walleye pollock and Atka mackerel fisheries in the Bering Sea, Aleutian Islands and Gulf of Alaska from 1977–92. U.S. Dep. Commer., AFSC Processed Report 93-08, 162 p.

[8] Nunnallee, E. P. 1991. An investigation of the avoidance reactions of Pacific whiting (*Merluccius productus*) to demersal and midwater trawl gear. ICES C.M. 1991/B:5, 16 p. [Available from Alaska Fisheries Science Center, NMFS/NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.]

[9] Hollowed, A. B., C. Wilson, M. Shima, and P. Walline. 2001. Study to determine the effect of commercial fishing on walleye pollock distribution and abundance. *In* Steller sea lion investigations, 2000 (B. S. Fadely, ed.), p. 89–104. U.S. Dep. of Commer., NOAA, NMFS, AFSC Processed Report 2001-05.

[10] NMFS (National Marine Fisheries Service). 1995. Status review of the United States Steller sea lion, *Eumetopias jubatus*, population. National Marine Mammal Laboratory, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, 61 p.

curred in the 1980s. However, it is important to keep in mind that pollock are only one component of the Steller sea lion diet and that all pollock survey data are collected during the summer.

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Movements of bocaccio (*Sebastes paucispinis*) and greenspotted (*S. chlorostictus*) rockfishes in a Monterey submarine canyon: implications for the design of marine reserves

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Abstract–In August and September of 1997 and 1998, we used SCUBA techniques to surgically implant Vemco V16 series acoustic transmitters in 6 greenspotted rockfish (*Sebastes chlorostictus*) and 16 bocaccio (*S. paucispinis*) on the flank of Soquel Canyon in Monterey Bay, California. Fish were captured at depths of 100–200 m and reeled up to a depth of approximately 20 m, where a team of SCUBA divers anesthetized and surgically implanted acoustic transmitters in them. Tagged fish were released on the seafloor at the location of catch. An array of recording receivers on the seafloor enabled the tracking of horizontal and vertical fish movements for a three-month period. Greenspotted rockfish tagged in 1997 exhibited almost no vertical movement and showed limited horizontal movement. Two of these tagged fish spent more than 90% of the time in a 0.58-km^2 area. Three other tagged greenspotted rockfish spent more than 60% of the time in a 1.6-km^2 area but displayed frequent horizontal movements of at least 3 km. Bocaccio exhibited somewhat greater movements. Of the 16 bocaccio tagged in 1998, 10 spent less than 10% of the time in the approximately 12-km^2 study area. One fish stayed in the study area for about 50% of the study time. Signals from the remaining 5 fish were recorded in the study area the entire time. Bocaccio frequently moved vertically 10–20 m and occasionally displayed vertical movements of 100 m or greater.

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Fish. Bull. 100:324–337 (2002).

Rockfishes (*Sebastes* spp.) are an important component of the commercial and recreational fisheries on the U.S. west coast. Recent stock assessments conducted by the Pacific Fishery Management Council (PFMC) have indicated large population declines for several species of rockfishes (PFMC[1]). For example, bocaccio (*Sebastes paucispinis*) abundance was estimated by MacCall et al.[2] to be 2–4% of pre-harvest levels, causing bocaccio to be formally designated as overfished by the U.S. National Marine Fisheries Service. This severe population decline prompted conservation organizations such as the World Conservation Union to consider bocaccio to be at high risk of extinction (IUCN, 1996). Even as management regulations have become more stringent, however, bocaccio populations continue to decline (MacCall et al.[2]).

As a result of these population declines, new management techniques, such as marine reserves, have been contemplated for west coast rockfishes (Yoklavich, 1998). Marine reserves currently are being considered as supplements to traditional fishery management schemes in many places around the world (Agardy, 1997; Allison et al., 1998). Marine reserves can serve as undisturbed areas for research, as regions designated for limited harvest, or as fishery exclusion zones where fishes can take refuge from exploitation (Murray et al., 1999). They also can serve as a buffer for management trials and as sources for recruits to fisheries (Johnson et al., 1999; Nowlis and Roberts, 1999). The effectiveness of marine reserves for conservation of heavily fished species, however, is dependent upon the size, shape, and location of reserves and on rates of movement of the protected species (Polacheck, 1990; DeMartini, 1993; Lauck et al., 1998). In this respect, an understanding of the rates and directions of daily movements of rockfishes is vital to understanding the value of marine reserves for these species (Carr et al., 1998; Starr, 1998).

[1] PFMC (Pacific Fishery Management Council). 1999. Status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000: stock assessment and fishery evaluation. Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, OR.

[2] MacCall, A. D., S. Ralston, D. Pearson, and E. Williams. 1999. Status of bocaccio off California in 1999 and outlook for the next millenium. *In* Appendix: status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000: stock assessment and fishery evaluation. Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, OR.

Few studies have described the movements of commercially caught rockfishes in water deeper than 100 m, however, because of the difficulty in achieving high survival rates for fish tagged at those depths. Most rockfishes have physoclistous swim bladders that expand with the reduced pressure as these fish are brought to the surface. The resulting barotrauma causes death for almost all fish when captured from waters deeper than 20–30 m, rendering traditional tagging techniques ineffective.

We developed techniques to surgically implant sonic transmitters at depth, thus reducing tagging mortality (Starr et al., 2000). These techniques enabled us to estimate the movements of two rockfishes with different life history characteristics. In 1997, we placed sonic transmitters in six greenspotted (*S. chlorostictus*) rockfish, a species presumed to be relatively sedentary (Yoklavich et al., 2000). In 1998, we tagged 16 bocaccio, a more mobile species (Love, 1996). In both years, we tracked the horizontal and vertical movements of tagged fish for a three-month period.

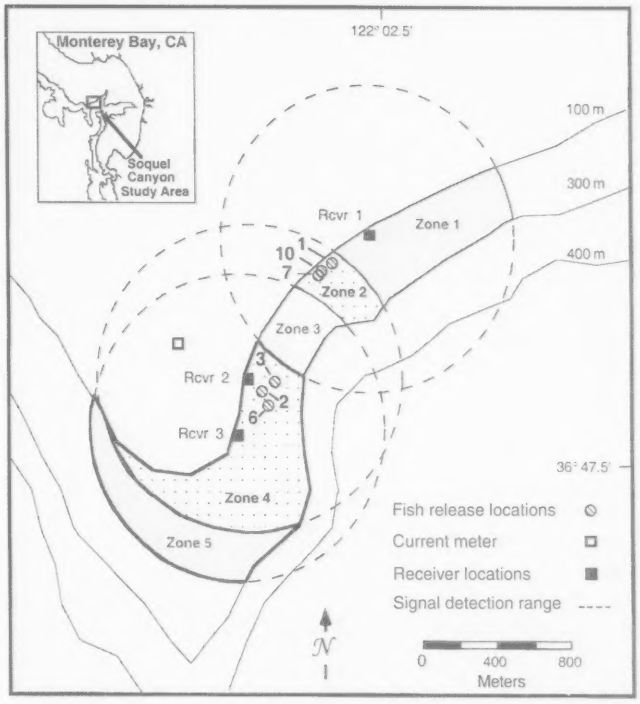

Figure 1

Fish-release locations and tag numbers, receiver locations, current meter location, expected signal detection range, and resulting receiving zones for the 1997 study of greenspotted rockfish.

Materials and methods

Field procedures

Our study site was located on the flank of the submerged Soquel Canyon in 100–250 m of water, approximately 20 km off shore in Monterey Bay, California (Fig. 1). Soquel Canyon contains steep sediment slopes and rock walls interspersed with 50–100 m wide benches. comprising soft sediment and rock outcrops (Yoklavich et al., 2000). Several of the rock outcrops located at the rim of the canyon are 10–20 m high by 50–100 m long scarps with boulders at the bases of the linear rock walls.

In 1997, we caught greenspotted rockfish using longline fishing gear deployed from a research vessel. In 1998, we hired a commercial fisherman to catch bocaccio using modified trolling gear. In both years, fishing lines were retrieved at about 20 m/min. Fishes were brought to a depth of about 20 m and held there for tagging. Divers then surgically implanted Vemco V16 (Vemco Ltd., Nova Scotia, Canada) sonic tags into the captured fish. Following surgery, tagged fish were placed in a recovery-release cage, then towed to the differential GPS location at which they were caught, whereupon the cage was lowered to the seafloor and fish were released. We used the *Delta* submersible to verify that tagged fish were alive after release. A more complete description of tagging and underwater tracking procedures is provided in Starr et al. (2000).

Vemco VR-20 receivers were moored on the seafloor for the duration of the study as a means of tracking tagged fish. The positions of receiver deployment spanned the distribution of release locations of the tagged fish. To increase the amount of positional information available from the receiver data, we placed the tagged fish and receivers along the side of a submarine canyon that stretched northeast to southwest. On 7 October 1997, we placed three receivers on a ledge at a depth of about 160 m along the wall of the canyon (Fig. 1). The receivers spanned a distance of 1500 m and recorded signals for 6 minutes out of every half-hour. We retrieved them on 5 January 1998.

In 1998, we deployed two receivers on surface buoys from 17 August through 10 September because tagging operations commenced one month before the submersible was scheduled to deploy the underwater moorings. These receivers were placed near the locations at which fish were released, in the northeastern portion of the Soquel Canyon study area (site 1, Fig. 2) and in the southwestern portion of the study area (site 2, Fig. 2). On 16 September 1998, we placed six receivers at various depths about 1000 m apart (Fig. 2) and retrieved them on 30 December 1998. Two of the receivers were located in about 100 m of water on the relatively flat substrate above the canyon rim. The other four receivers were placed in deeper water on flat benches or gently sloping walls below the canyon rim. These receivers recorded signals for 12 minutes every hour. In both years, battery life of the tags exceeded the length of time the receivers were moored.

Signal detection range of the moored receivers was about 800 m (Starr et al. 2000). Thus, if a signal was recorded at a particular time by only one receiver, we knew

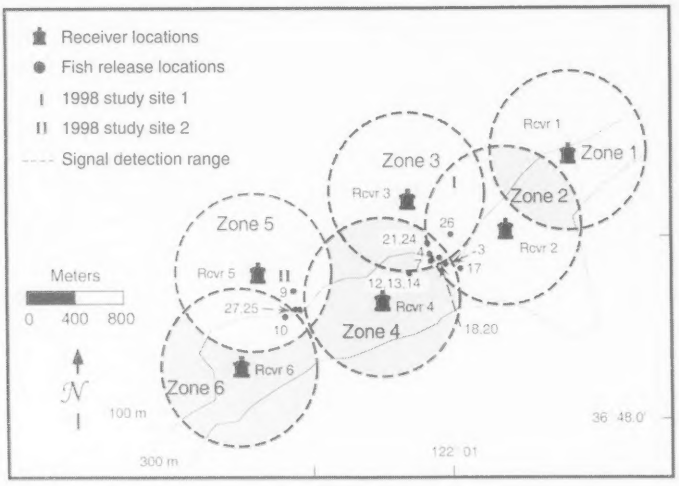

Figure 2

Fish-release locations with tag numbers, receiver locations, current meter location (moored with receiver 1), expected signal detection range, and resulting receiving zones for the 1998 field study of bocaccio.

Table 1

Patterns of signal receptions that define "receiving zones." Signals recorded concurently by the listed combinations of receivers were assigned a receiving zone that represents an approximate location of a tagged fish in a specified time period.

1997		1998	
Receivers (by receiver number) that recorded signals	Receiving zone no.	Receivers (by receiver number) that recorded signals	Receiving zone no.
1	1	1	1
1,2	2	1,2	2
2	3	2	3
2,3	4	2,3	3
3	5	2,3,4	3
		2,4	3
		3	3
		3,4	4
		4	4
		4,5	5
		5	5
		5,6	5
		6	6

the tag was located within 800 m of that receiver and outside the range of detection of other receivers. If a signal was recorded at the same time by two or more receivers, we knew the tag was somewhere within the intersection of the circles that represented the overlap of detection range for the respective receivers. We defined the combinations of intersections or exclusions of overlapping 800-m detection ranges as "receiving zones." In 1997, five such receiving zones were detected (Table 1). We labeled the northeasternmost receiving zone (signals only recorded by receiver 1) as zone 1. Zone numbers increased to the southwest. Because we knew the depths of all the greenspotted rockfish tracked in 1997, we were able to refine estimated locations of a tag to the area in each receiving zone that was between the 100–300 m isobaths (Fig. 1).

In 1998, the same method provided 13 combinations of overlapping detection ranges—too many to permit the patterns of fish movement to be understood easily. Consequently, we grouped combinations of overlapping detection ranges into six receiving zones by their spatial distribution

(Table 1). This enabled us to use signal location and tag depth data to more effectively estimate fish positions and movements. Again, the most northeastern receiving zone (signals only recorded by receiver 1) was labeled as zone 1; zone numbers increased to the southwest (Table 1, Fig. 2).

Each year we placed an S-4 current meter with recording thermometer and salinometer on a mooring near the seafloor to determine if changes in current, salinity, or temperature affected fish movement. In 1997, the current meter was located in 100 m of water on the shelf about 400 m away from receiver 2 (Fig. 1). In 1998, the current meter was moored with receiver 1, and was located in 100 m of water (Fig. 2).

Data analysis

Receivers logged the tag number, date, time of day, acoustic frequency, and tag depth each time a signal was detected. Receivers also recorded signal strength, noise, gain, and error messages provided by the receiver software. Data collected by the moored receivers were downloaded as text files and imported into a database for analysis. Tag depth was plotted versus time of signal reception for each tag and each receiver. Differences in fish depths by time of day were analyzed with ANOVA and Scheffe's *F*-test *post-hoc* analysis (Sokal and Rohlf, 1997).

In 1997, we grouped signals into half-hour time intervals to compare signal receptions between receivers. In 1998, we grouped signals into hourly intervals. We labeled each interval a time "bin" and standardized bin numbers among all receivers. Thus, any signal recorded by a receiver in a given time period (bin) could be directly compared with signals from other receivers in similar time bins. In 1997, the study included 4309 half-hour time bins. In 1998, the study included 2535 hourly time bins.

Each signal was thus assigned a time bin and a receiving zone according to the time interval of signal reception and the combination of receivers recording signals from that tag number. Treating each receiving zone number as a numeric rank enabled us to use a simple average of rank to identify the predominant receiving zone that a fish occupied in the time bins that occurred during a week (336 weekly bins in 1997 and 118 weekly bins in 1998). A difference in average ranking among weeks indicated the fish had moved; the value of the average indicated the direction in which the fish moved. For each tag, a chi-square test of heterogeneity was used to test for differences in average ranking among weeks. In 1997, week 2 of the study was the first week for which there were transmissions from all tagged fish; thus week 2 was used to represent the expected fish distribution by receiving zone for the chi-square test. In 1998, we used week 1 to represent the expected distribution. We also used the unplanned test of homogeneity of replicates tested for goodness of fit (Sokal and Rohlf, 1997) to determine if the average location of a fish (average rank) was similar between weeks. This method enabled us to group weeks in which a fish was in a similar location. In addition to generating weekly distributions, we used the ranking system to plot semihourly (1997) or hourly (1998) movements of tagged fish.

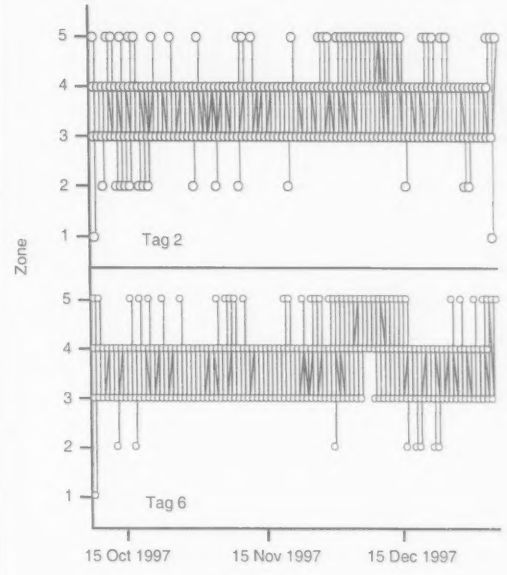

Figure 3

Movements of tagged greenspotted rockfish (tag-2 and tag-6 fish) across study area in 1997, as depicted by changes in receiving zones that were derived from patterns of signal receptions.

Results

Greenspotted rockfish

In 1997, we tagged six greenspotted rockfish, ranging in total length from 35 to 39 cm (Starr et al., 2000). Lea et al. (1999) reported that greenspotted rockfish in this size range are 11–15 yr old and probably mature. The three moored receivers recorded signals throughout the study period from all tags except tag 1. Signals from tag 1 were recorded for 18 hours, then not again until 67 days later. The total number of transmissions recorded from each tagged fish ranged from 156 to 24,132 (Starr et al., 2000).

Except for tag-1 fish, tagged greenspotted rockfish exhibited two patterns of relatively small horizontal movements. Tag-2 and tag-6 fish remained primarily in the receiving zone in which they were released (zone 4) and exhibited few cross-zone movements (Fig. 3, Table 2). Receivers recorded transmissions from each of these tags in 99% of the time bins. More than 56% of the time, signals originated in receiving zone 4, and 94% of the time signals originated from receiving zones 3 or 4 (Table 2), an area comprising 58 ha, or a linear distance along a ledge of 1200 m. When the fish moved out of zones 3 or 4, they most often moved southwest, towards the mouth of Soquel Canyon (towards Zone 5 in Fig. 3). Chi-square and *post-hoc* analyses indicated similarity in the pattern of signals received from the tags for most weeks, as indicated by the weekly average rank of receiving zone (Fig. 4).

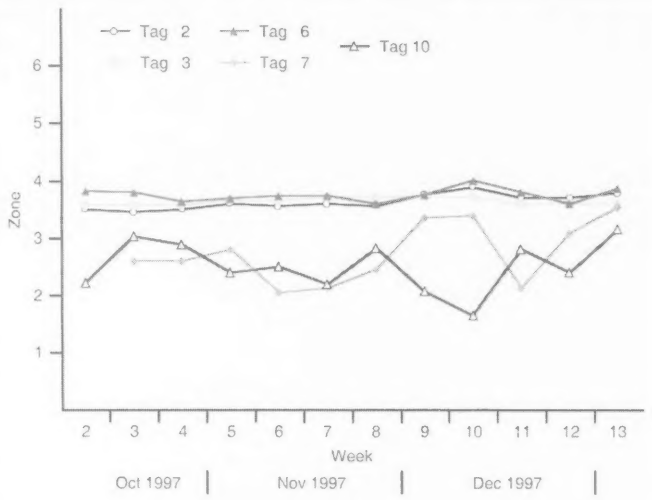

Figure 4

Distribution of tagged greenspotted rockfish in 1997 as depicted by the weekly average rank calculated from receiving zones which were derived from patterns of signal receptions.

Table 2

Percentage of half-hour time bins by receiving zone in which signals were recorded from tagged greenspotted rockfish from 7 October 1997 through 5 January 1998. None = the percentage of time bins in which no signal was recorded.

	Zone number					
Tag number	1	2	3	4	5	None
1	0.1	0.2	0.4	0.3	0.1	98.8
2	0.0	0.4	37.9	56.2	4.4	1.0
3	2.0	3.6	26.5	28.2	14.1	25.6
6	0.0	0.2	26.4	67.3	5.1	1.0
7	11.6	9.6	24.2	8.1	5.2	41.2
10	11.2	12.7	31.6	6.9	2.6	35.0
Zone area (ha)	53.3	11.4	3.9	54.0	36.4	

Table 3

Frequency of time lapse between signals after a time bin in which no receivers recorded signals from tagged greenspotted rockfish in 1997. NA = no signal was recorded for 67 days.

Tag number	0–1 h	1–5 h	5–10 h	>10 h	Max. time (h)
1	NA	NA	NA	NA	
2	7	1	0	0	1.5[1]
3	368	102	7	2	12.5[1]
6	6	0	0	0	1[1]
7	253	107	14	16	30
10	296	101	19	6	27.5

[1] Signals from these fish were not recorded for the first 17 h that receivers were in place and are not included in this table. Signals may not have been recorded because of electronic interference from boats in the area that prevented receivers from recording signals. The other two fish (tag-7 and tag-10 fish) were released a week after receivers were in place.

Tag-3, tag-7, and tag-10 fish moved greater distances, and made relatively frequent short-term movements out of the zone in which they were originally tagged and released (Fig. 5, Table 2). For these tags, 26–41% of the time bins contained no signals. The maximum time recorded for a tag in a single receiving zone was 32% of the time bins, and at least three zones were needed to account for 60% of the signals received from each tag. All three tagged fish showed evidence of moving across the entire study zone, a linear distance of 2940 m, and an area of about 1.6 km^2. Chi-square and *post-hoc* analyses indicated there were significant (P<0.05) differences in the weekly average rank of receiving zone for tags 3, 7, and 10 (Fig. 4). Transmissions from these tags were frequently recorded in all receiving zones (Fig. 5) and the fish also moved out of the study area for short time periods. The maximum time between recorded signals from any of these tags was 30 h. More than 90% of the time, the interval between recorded signals was 5 hours or less (Table 3).

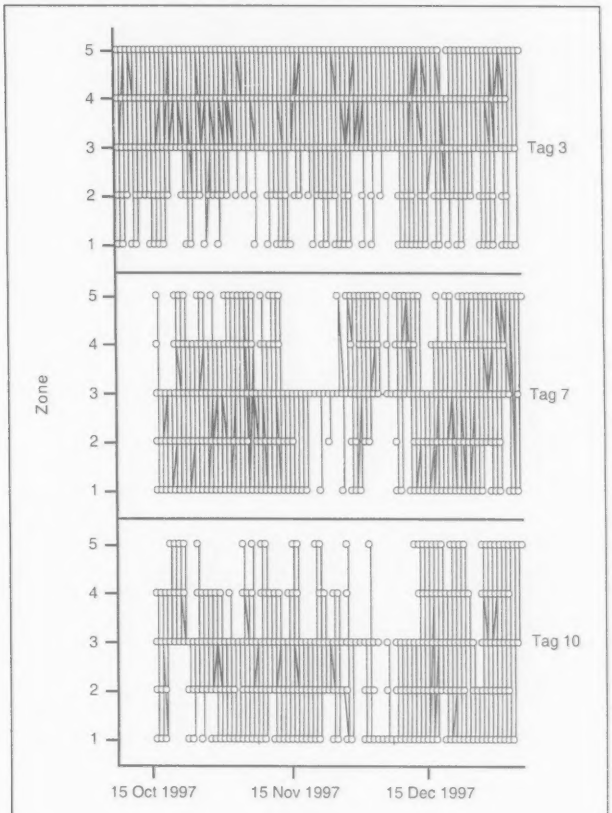

Figure 5

Movements of tagged greenspotted rockfish (tag-3, tag-7, and tag-10 fish) across the study area in 1997 as depicted by changes in receiving zones which were derived from patterns of signal receptions.

All tagged greenspotted rockfish, except tag-1 fish, showed little vertical movement, and 99% of depth transmissions from each tag were within ±3 m (see Fig. 6 for an example of this pattern). This distance is effectively the range of tidal variation and the error associated with the depth sensors in the sonic tags. Some of the fish occasionally made short-term movements to deeper locations. The only exception to this pattern was tag-1 fish that was tracked for 18 hours, lost, then heard again 67 days later. It exhibited vertical movements of about 90 m in the hours before it left the study area (Fig. 7).

Bocaccio

In 1998 we tagged 16 bocaccio, ranging in length from 35 to 58 cm (Starr et al., 2000). Ten of the bocaccio we tagged were larger than the size at 50% maturity reported by Gunderson et al. (1980). The receivers placed on surface buoys in August and early September recorded continuously; the total number of transmissions recorded from each of the tags in that time bin ranged from 0 to 9531 (Starr et al., 2000). The total number of signals recorded by the six subsurface receivers that were deployed from 16 September through 30 December ranged from 0 to 19,213 (Starr et al., 2000). Ten of the tagged bocaccio spent little time in the 12-km^2 study area (Fig. 8). Signals from three tags were recorded only within a few days after tagging and were not heard again (tags 13, 24, 26), either because the fish left the study area or the tags failed to send signals. Lengths of these fish ranged from 47 to 51 cm (Starr et al., 2000). Transmissions from five tags were recorded in the study area for only 1–4 weeks (tags 3, 4, 10, 12, 21). Lengths of these tagged fish ranged from 35 to 52 cm. Three fish appeared to leave the study area and return two weeks to a month later (tags 17, 20, 25). Lengths of these fish ranged from 45 to 55 cm. Signals from the remaining five tags (tags 7, 9, 14, 18, 27) were recorded in the study area the entire time. Lengths of these fish ranged from 47 to 58 cm.

Signals from 10 tags were recorded in less than 10% of the time bins in any zone (Table 4). Signals from one tag

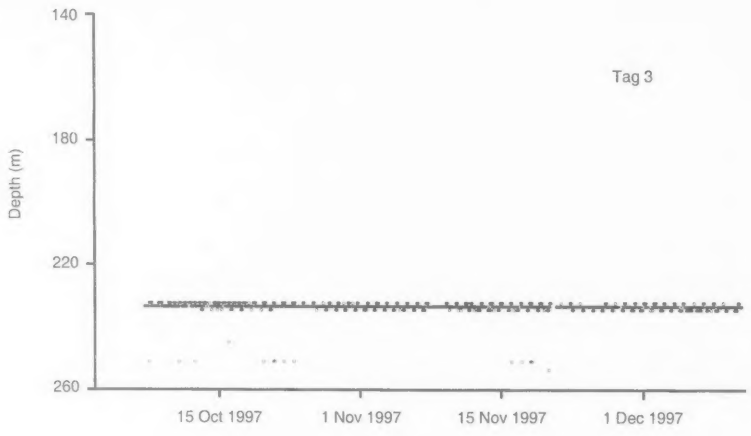

Figure 6

Depth distribution of signals received from tag 3 in 1997. Tag 3 is presented as an example of the depth distributions observed from all tagged greenspotted rockfish, except those of tag 1.

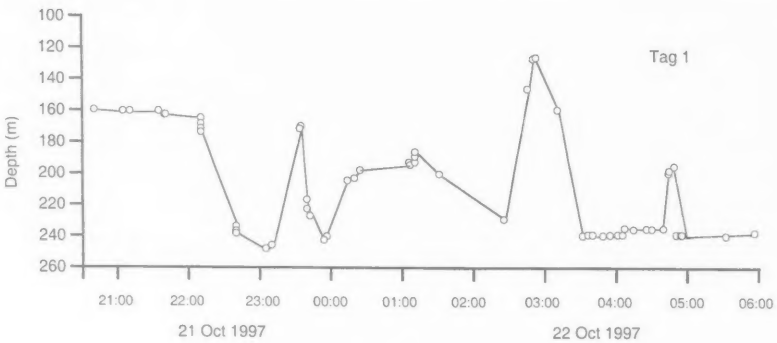

Figure 7

Depth distribution of signals received from tag-1 greenspotted rockfish in 1997.

were recorded about 50% of the time, and transmissions from the remaining five tags were recorded in more than 80% of the time bins. The six fish that remained in the study area 50% of the time or more stayed in a small part of the study area (Table 4). Signals from each of four tags (tags 9, 14, 17, 27) were recorded almost exclusively only where they were released, in receiving zones 4 or 5. These receiving zones comprised an area of 168 ha and 201 ha, respectively. Signals from the other two fish (i.e. tags 7, 18) were recorded primarily in receiving zones 3 and 4, an area of about 400 ha. Chi-square and *post-hoc* analyses indicated all fish stayed primarily in the same receiving zones for the time they were in the study area (Fig. 9).

Although the six fish that stayed in the study area stayed primarily in one or two receiving zones, they often exhibited small movements. Plots of zone numbers of recorded signals indicated that two of the fish (tags 7, 18) frequently moved across all receiving zones (Fig. 10). Additionally, cross-talk from receivers 5 and 6 indicated that tag-27 fish made frequent short-term movements (Starr et al., 2000). Tagged fish also occasionally left the study area. Except for tag 17, which was not recorded in the study area for 27 days, the maximum time interval between recorded signals from any of these tags was 57 h. More than 90% of the time, the interval between recorded signals was 5 h or less (Table 5).

Eight of the 16 tags transmitted information about depth. We recorded signals from five of the eight tags for only short time periods after the fish were released. Two of these five fish (tag-3 and tag-12 fish) moved vertically to within 15 m of the surface 9–12 hours after tagging, then returned below a depth of 90 m for a 12–15 day period before signals were lost (see Fig. 11 for an example of tag-3 fish movements). A third fish (tag-4 fish) fluctuated ±10 m around a depth of 90 m for a week, moved vertically to a depth of 14 m, and returned to a depth of about 90 m for another three weeks before signals ceased. A fourth tag (tag 13) was recorded for 3 days and exhibited frequent fluctuations of 20 m in depth before signals ceased.

Data from the remaining three fish containing depth transmitters were recorded throughout the study. Depth transmissions from tag 14 varied less than 3 m, whereas depth transmissions from tag 7 (Fig. 12) and tag 9 (Fig. 13) indicated cyclical vertical movements of ±10–20 m, and occasional deeper dives. The greatest variation in depth was exhibited from tag 7. That fish made several dives of 100 m; once it moved from 100 m to 220 m and back in a 20-h period. Tag-7 and tag-9 fish also demonstrated a diurnal periodicity in vertical movements. Fish were more active and higher during the day and less active and deeper at night (Fig. 14). The ANOVA and Scheffe's *F* test statistics indicated significant differences in both depth and change in depth between dawn, day, dusk, and night hours (Table 6).

Environmental parameters fluctuated but did not appear to be related to fish movements. Salinity and temperature data from the S-4 current meter at 100-m depth fluctuated within 24-h periods, but there were no obvious trends within or between years. Salinity averaged 33 ppt in 1997 and 34.5 ppt in 1998. Water temperature fluctuated from 10 to 15°C in 1997, whereas in 1998 it was more consistent, ranging from 9 to 11°C. Current speed and direction fluctuated in what appeared to be a tidal basis (Shea and Broenkow, 1982), but since there was no obvious relationship to recorded movements, this relationship was not explored in more detail.

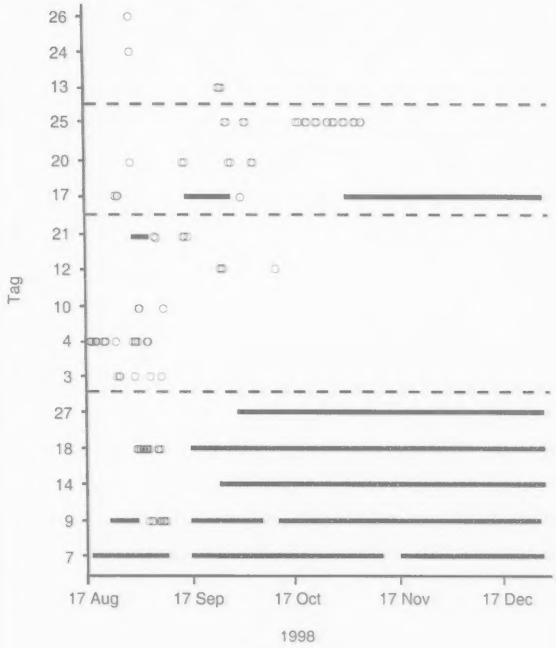

Figure 8

Dates of signal receptions in study area from sonic transmitters implanted in bocaccio in 1998. Circles represent individual occurrences of recorded signals; solid lines represent almost continuous occurrences of recorded signals. Dashed lines on the graph are shown to separate the groups of tagged fish discussed in the text.

Discussion

Fish movements

The *in situ* tagging procedures we developed alleviated many problems associated with surface tagging and provided means for tracking deeper-water rockfishes. We expected greenspotted rockfish to move only small distances because of their affinity to seafloor habitats such as overhangs and crevices (Stein et al., 1992; Yoklavich et al., 2000). Our work confirmed that greenspotted rockfish are relatively sedentary. The greenspotted rockfish we tagged with depth transmitters moved less than ±3 m vertically during the study, except for a few occasions when a fish swam down 20–40 m, only to return to its original depth within 2 hours. This small variation in depth displayed by the tagged greenspotted rockfish indicated that these fish most likely do not leave canyon wall habitats to feed. Love (1996) indicated that they eat mainly small invertebrates, but also cephalopods and fishes. It is possible that prey in the water column is advected toward them along the canyon wall (Isaacs and Schwartzlose, 1965; Genin et al., 1988). They do not appear to migrate vertically to feed on scattering layer organisms as do other rockfishes such as yellowtail rockfish (*Sebastes flavidus*) off Oregon (Pereyra et al., 1969).

Horizontal movements of the tagged greenspotted rockfish were on the order of hundreds of meters to a few kilometers. Receivers 2 and 3 each recorded cross-talk from signals of the same two tags (tags 2, 6) at several different times, indicating that these fish alternately swam close to one receiver, then at a later time swam close to a second receiver that was more than 300 m away (Starr et al., 2000). Although most movements were contained well within the 3-km long study area, half of the fish made sojourns out of the study area for short time periods. We think these small, short-term movements represent foraging activity along the canyon ledge.

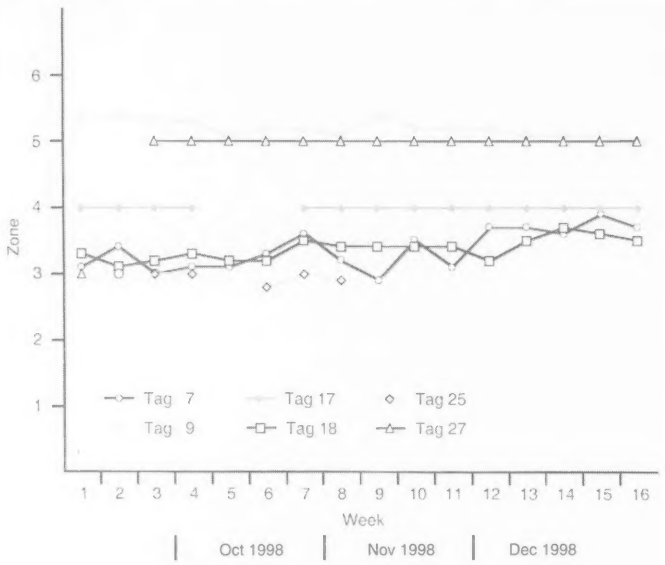

Figure 9

Distribution of six tagged bocaccio in 1998 as depicted by the weekly average rank calculated from receiving zones derived from patterns of signal receptions.

Table 4

Percentage of hourly receiving bins in which signals from tagged bocaccio were recorded from 16 September through 30 December 1998. None = the percentage of time bins in which no signal was recorded.

Tag number	Zone number						None
	1	2	3	4	5	6	
3	0.0	0.0	0.0	0.0	0.0	0.0	100.0
4	0.0	0.0	0.0	0.0	0.0	0.0	100.0
7	3.3	3.8	41.5	35.3	1.7	0.7	13.7
9	0.0	0.0	0.0	0.2	67.5	17.6	14.7
10	0.0	0.0	0.0	0.0	0.0	0.0	100.0
12	0.0	0.0	0.2	0.4	0.1	0.1	99.2
13	0.0	0.0	0.2	0.4	0.1	0.1	99.2
14	0.0	0.0	0.1	98.0	0.5	0.0	1.4
17	0.0	0.0	0.0	50.4	0.0	0.0	49.6
18	2.0	8.7	29.6	39.3	2.0	0.0	18.4
20	0.0	0.0	0.2	0.0	0.5	0.1	99.3
21	0.0	0.0	0.4	0.4	1.3	0.0	97.9
24	0.0	0.0	0.0	0.0	0.1	0.0	99.9
25	0.3	0.0	5.1	0.0	0.0	0.0	94.7
26	0.0	0.0	0.0	0.0	0.0	0.0	100.0
27	0.0	0.0	0.0	0.0	99.7	0.0	0.3
Zone area (ha)	124.0	75.5	232.2	168.0	201.0	132.4	

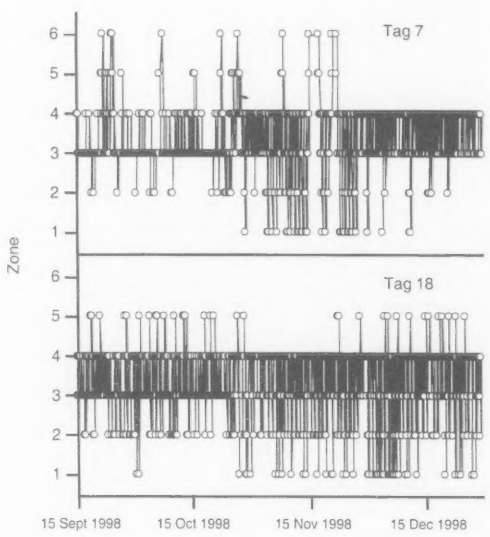

Figure 10

Movements of tag-7 and tag-18 bocaccio across the study area in 1998 as depicted by changes in receiving zones derived from patterns of signal receptions.

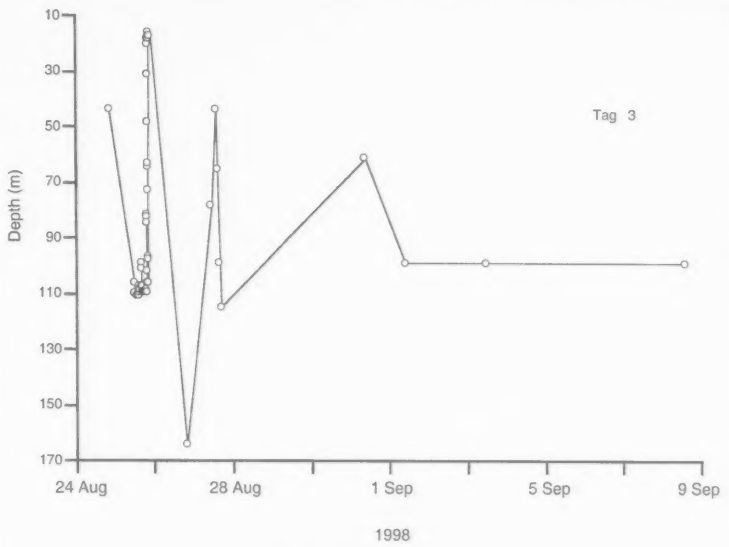

Figure 11

Depth distribution of signals received from tag-3 bocaccio in 1998. Tag-12 bocaccio displayed a similar pattern.

We expected bocaccio to move more than greenspotted rockfish. Bocaccio are frequently caught in midwater trawl nets and are considered more mobile than greenspotted rockfish (Love, 1996). Hartman (1987) reported that juvenile bocaccio moved a maximum of 148 km over two years in tag-recapture studies in southern California. In this respect, young bocaccio are similar to yellowtail rockfish (*Sebastes flavidus*) that have exhibited movements on the scale of hundreds of kilometers in tag-recapture studies conducted in Alaska and British Columbia (Stanley et al., 1994). In Stanley et al.'s studies, 75% of the tag recoveries were within 25 km of the release point, but maximum movement observed was 250 km for Canadian yellowtail rockfish, and 1400 km for Alaskan fish.

Not all studies have shown that yellowtail rockfish move great distances, however. Using ultrasonic telemetry, Pearcy (1992) tracked them from the surface intermittently for periods of several days and reported that tagged fish generally stayed within 2 km of the capture or release location. After a period of 13 days in 1990, 11 of 12 tagged fish were detected within 300 m of the capture site, even though some fish had been displaced. A month after release, eight of 12 tagged fish were within 1.4 km of the capture location.

Pearcy (1992) also suggested that the tagged fish exhibited site fidelity to a pinnacle habitat. Pearcy's work, combined with results from other displacement studies (Carlson and Haight, 1972; Hallacher, 1984; Matthews, 1990; Heilprin, 1992), suggests that several species of rockfish possess homing ability. Half of the bocaccio we tagged either stayed in the study area during the entire time of the study, or left and returned, suggesting some site fidelity. Evidence of site fidelity was also provided by the chi-square analyses of fish location in receiving zones. The analyses indicated that bocaccio remained in the same area over the course of a week, despite the evidence of frequent movements out of a receiving zone on a daily basis.

Table 5

Frequency of time lapse between recorded signals after a time bin in which no receivers recorded signals from tagged bocaccio in 1998. Only tagged fish that remained in the study area for more than 50% of the time are shown.

Tag number	0–1 h	1–5 h	5–10 h	>10 h	Max. time (h)
7	115	30	6	3	57
9	152	66	1	2	28
14	14	2	0	0	1
17	143	86	10	5	660
18	201	86	2	1	12
27	2	0	0	0	1

Although our study was designed to evaluate the residence time of bocaccio in a discrete area, and not to quantify the maximum distance bocaccio move, the relatively small percentage of tagged bocaccio that stayed in our 12-km^2 study area during the entire study period indicated that bocaccio may also move large distances. The results of our study tend to reinforce the hypothesis presented

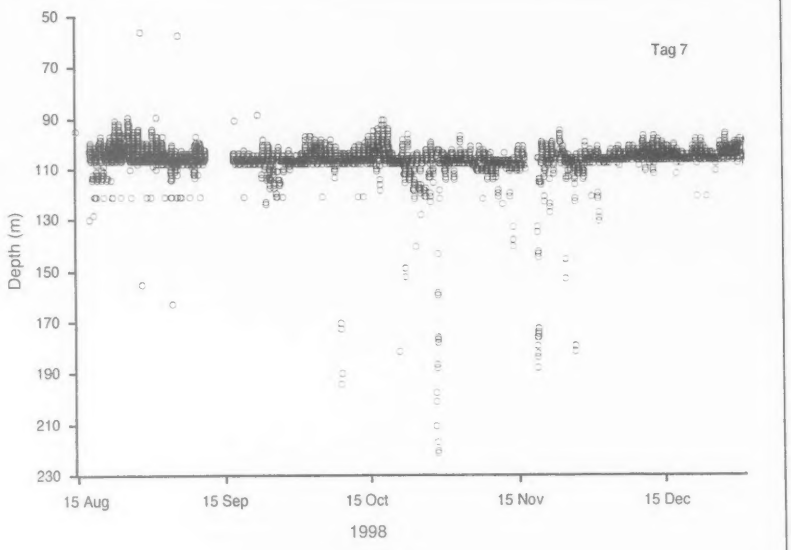

Figure 12
Depth distribution of signals received from tag-7 bocaccio in 1998.

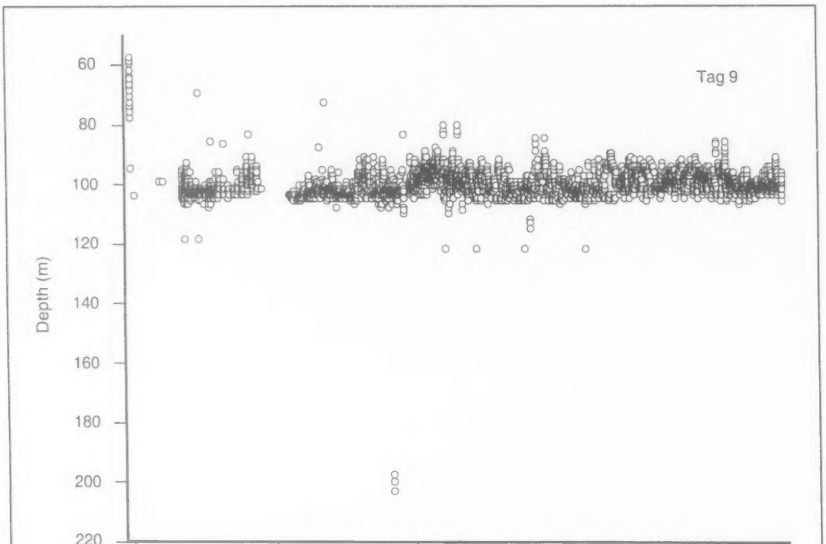

Figure 13
Depth distribution of signals received from tag-9 bocaccio in 1998.

(MacCall[2]) that there are two types of observed movements of bocaccio: pelagic and "refugial." They suggested, from observations of the large sizes of bocaccio observed as single individuals and the occurrence of smaller animals in mid-water trawl catches, that there may be an ontogenic shift from pelagic to refugial habits. They hypothesized

that subadults are more mobile than adults, and as the fish increase in size, they become more sedentary. From tag transmissions and submersible surveys, we observed both pelagic and refugial behavior (about 25% of the tagged animals exhibited refugial behavior). The two largest tagged bocaccio were among the five fish that moved the least. The narrow size range of most of the tagged fish, however, precluded an analysis of movements by fish length.

Tagged bocaccio made frequent small vertical movements that were associated with time of day. The magnitude of the vertical movements matched the vertical relief of the habitats used by tagged fish. During submersible operations, we tracked tagged fish in small schools as they moved along rock scarps that were 10–20 m high and 100–200 m long (Starr et al., 2000). These scarps were often at, or just below, the rim of the submarine canyon. The depth transmissions from tags indicated that fish were at the top or just above the rock habitats during the day, and lower and more sedentary at night. We attribute the increased activity during the day to the fact that bocaccio are visual predators (Love, 1996) and are thus more apt to forage during the day.

Four of the eight fish containing depth transmitters made rapid vertical movements. Three of the bocaccio rose vertically to spend a short time near the surface, then returned to depths from which they came. These fish all remained only a few weeks in the study area. A fourth fish made a deep dive to 220 m and back to 100 m in less than a day (Fig. 12). The purposes of these dives are unknown, but such dives reinforce our observations during tagging operations that bocaccio can modify the volume of air in their swim bladder. Pearcy (1992) observed that yellowtail rockfish also are capable of discharging air from their swim bladders in a relatively short time.

For some tags, there were short time intervals when signals were not recorded. This may have been caused by the canyon topography or by fish behavior. The complex topography of Soquel Canyon and the behavior of the rockfishes may have prevented the receivers from receiving all possible transmissions from tagged fish. The hard, steep walls that undulate along the side of the canyon (Yoklavich et al., 2000) occasionally cause echoes and an original transmission to coincide, thus preventing the receivers from recording a valid signal. Other signal lapses may also have been due to the tendency of rockfish to take shelter under rocks or ledges. From the surface, we occasionally heard weak signals that were unusually high-pitched and that sounded "tinny." We have experienced the same type of reception when tracking shallow-water rockfishes that took shelter under a rock or ledge. Signals return to full strength and timbre when the fish leaves the crevice.

Table 6

Results of Scheffe's *F post-hoc* test (*P* values) were used to identify differences in fish depth between different times of the day (i.e. between dawn and day [dawn–day], dawn and dusk [dawn–dusk], etc.) or diel differences in depth and change in depth of signal receptions from tagged bocaccio (tag-7 and tag-9 fish) in 1998.

	Tag 7		Tag 9	
	Depth	Change in depth	Depth	Change in depth
Dawn–day	0.0097	0.0194	<0.0001	<0.0001
Dawn–dusk	0.2840	0.277	0.0040	0.0004
Dawn–night	0.5045	<0.0001	<0.0001	<0.0001
Day–dusk	0.7455	0.9031	0.7312	0.9998
Day–night	<0.0001	0.0065	0.1010	<0.0001
Dusk–night	0.0007	0.0156	0.0440	<0.0001

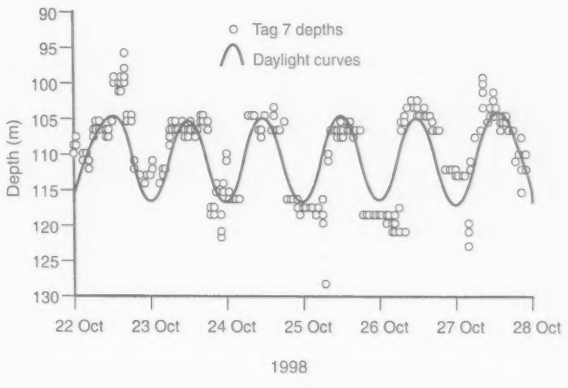

Figure 14

Depth transmissions recorded for tag-7 bocaccio plotted with daylight curve for the period 22–28 October 1998.

Implications for marine reserves

Tag-recapture studies of shallow water (<100 m) demersal rockfishes typically have indicated very little movement; only one species in ten studies exhibited long-term movements greater than 3 km (Stanley et al. 1994; Lea et al., 1999). Results from these studies support the idea that small harvest refugia may effectively protect nearshore rockfishes. This would be fortuitous if almost all nearshore rockfishes have small home ranges, because most of the marine reserves in the eastern Pacific Ocean are very small and have been created without regard to typical movements of species (McArdle, 1997; Starr, 1998; Yoklavich, 1998).

Our results indicate a considerable short-term variation in the movements of individual greenspotted rockfish, which may be masked by the long-term nature of tag-recapture studies. Although almost all fish may remain in a small area over the course of several years, an individual

fish may occasionally move longer distances. This raises a question about the efficacy of marine reserves that are designed to account for modal distributions of fish based on traditional tag-recapture studies.

The efficacy of a marine reserve is directly related to its size and shape and the movements of the protected species (Polacheck, 1990; DeMartini, 1993; Nowlis and Roberts, 1999). Thus, without estimates of both the range and frequency of movements of the target species, it is difficult to predict the effectiveness of a reserve for conserving fishes (Carr and Raimondi, 1998). Infrequent foraging excursions out of a reserve, for example, could potentially negate the value of a reserve if its purpose is to act as a harvest refugium. Conversely, small home ranges could preclude a "spillover" effect and diminish a reserve's ability to enhance local fisheries, if that were the goal. Small reserves may appear to protect species that move little, but if protected fishes occasionally move greater distances, as did the tagged bocaccio and greenspotted rockfishes in our study, then larger reserves may be needed to encompass 90% or more of the typical monthly movements of a species. Models that incorporate movement into the theoretical design and evaluation of marine reserves may thus be strengthened by using the probability or percentage of time an animal actually remains in the reserve boundaries rather than modal distributions. The periodic departure of tagged fish from their center of activity suggests that a conservative strategy for the design of marine reserves would be to include a buffer zone to account for these infrequent sojourns.

Only one-fourth of the tagged bocaccio spent more than 80% of their time in the 12-km^2 study area. Yet the Soquel Canyon study area was two times larger than the mean size and four times larger than 70% of marine reserves in California that regulate fishing in any way (McArdle, 1997). Such movement will require that marine reserves intended to effectively protect bocaccio will need to be much larger than most current reserves. Until the full extent of the range and periodicity of movements is known, however, it will be difficult to adequately design a system of marine reserves to protect bocaccio stocks.

After tagging, greenspotted rockfishes returned to rock habitats on the ledges at the side of Soquel Canyon and exhibited small horizontal and vertical movements. Based on the signal receptions for our three-month period, the size of a marine reserve would need to have a diameter of 3 km to account for 95% of the typical movements of the tagged greenspotted rockfish. Bocaccio, however, returned to higher relief habitats near the canyon rim after release and exhibited much greater horizontal and vertical movements. An effective reserve for bocaccio, therefore, would need to be larger than the 12 km^2 area encompassed by our study.

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Efficiency of bycatch reduction devices in small otter trawls used in the Florida shrimp fishery

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Abstract–Two bycatch reduction devices (BRDs)—the extended mesh funnel (EMF) and the Florida fisheye (FFE)—were evaluated in otter trawls with net mouth circumferences of 14 m, 17 m, and 20 m and total net areas of 45 m^2. Each test net was towed 20 times in parallel with a control net that had the same dimensions and configuration but no BRD. Both BRDs were tested at night during fall 1996 and winter 1997 in Tampa Bay, Florida. Usually, the bycatch was composed principally of finfish (44 species were captured); horseshoe crabs and blue crabs seasonally predominated in some trawls. Ten finfish species composed 92% of the total finfish catch; commercially or recreationally valuable species accounted for 7% of the catch. Mean finfish size in the BRD-equipped nets was usually slightly smaller than that in the control nets. Compared with the corresponding control nets, both biomass and number of finfish were almost always less in the BRD-equipped nets but neither shrimp number nor biomass were significantly reduced. The differences in proportions of both shrimp and finfish catch between the BRD-equipped and control nets varied between seasons and among net sizes, and differences in finfish catch were specific for each BRD type and season. In winter, shrimp catch was highest and size range of shrimp was greater than in fall. Season-specific differences in shrimp catch among the BRD types occurred only in the 14-m, EMF nets. Finfish bycatch species composition was also highly seasonal; each species was captured mainly during only one season. However, regardless of the finfish composition, the shrimp catch was relatively constant. In part as a result of this study, the State of Florida now requires the use of BRDs in state waters.

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Commercial fishermen use a variety of gears to harvest shrimp in southeastern U.S. waters, but they have predominantly used the otter trawl since the 1940s. The otter trawl is an unselective gear that commonly has an associated catch of untargeted organisms (e.g. finfish, miscellaneous invertebrates) that are referred to as "bycatch." Numerous definitions for the term " bycatch" have been proposed (Allsopp, 1982; Caddy, 1982; Saila, 1983). The most comprehensive, suggested by Alverson et al. (1994), refers to nontargeted species retained, sold, or discarded for any reason.

An estimated average of 27.0 million metric tons (t) (range=17.9–39.5 million t) of bycatch are discarded annually by the world's marine fishing fleets (Alverson et al., 1994). Shellfish fisheries compose 14 of the top 20 fisheries worldwide in quantity of bycatch discards (Alverson et al., 1994) and account for 9.5 million t of discards annually. Because the harvest of bycatch often exceeds that of the targeted species, the issue of bycatch in marine fisheries has become a global concern.

In the southeastern United States, the penaeid shrimp fishery often ranks first in value of all fisheries for commercially harvested marine species. In 1996, total landings were 98 million kg and were valued at approximately $434 million, ex-vessel price (size-specific price per unit volume paid to the fisherman for the catch) (NMFS[1]). The Gulf of Mexico (referred to as "Gulf" in this study) shrimp fishery accounted for 90% of this volume and 87% of this value. In U.S. waters, the Gulf and the southeast U.S. Atlantic (referred to as "South Atlantic") shrimp trawl fisheries ranked 5th and 9th, respectively. Their ratios of kg finfish bycatch to kg shrimp were 10.3:1 for the Gulf, and 8.0:1 for the South Atlantic (Alverson et al., 1994). However, the Gulf and South Atlantic Fisheries Development Foundation (GSAFDF[2]) estimated that the ratio of finfish bycatch to shrimp harvest was 4.2:1 for the Gulf shrimp fishery and 2.8:1 for the South Atlantic shrimp fishery. Thus, using the more conservative ratios reported by GSAFDF and the 1996 shrimp landings for the Gulf fishery (88 million kg) and the south Atlantic fishery (9.9 million kg; NMFS[1]), the estimated total finfish bycatch for these two fisheries is 370 million kg and 28 million kg, respectively.

In 1996, approximately 11.3 million kg of shrimp were landed along the Florida Gulf coast and 1.8 million kg of shrimp were landed along the Florida Atlantic coast (NMFS[1]). Ratios of finfish bycatch to shrimp for the Florida Gulf coast ranged from 2.3:1 (fish-

[1] NMFS (National Marine Fisheries Service). 1997. Bycatch in the southeast shrimp trawl fishery. A data summary report. National Marine Fisheries Service, Southeast Science Center, 75 Virginia Beach Drive, Miami, FL 33149, 197 p.

[2] GSAFDF (Gulf and South Atlantic Fisheries Development Foundation). 1997. Bycatch and its reduction in the Gulf of Mexico and South Atlantic shrimp fishery. Final report to the National Oceanic and Atmospheric Administration (award NA57 FF0285). GFSFDF, Suite 997, Lincoln Center, 5401 West Kennedy Boulevard, Tampa, FL 33609, 27 p.

ing depth >10 fathoms [fm]) to 2.5:1 (fishing depth < 10 fm) (NMFS[1]); thus total finfish bycatch can be estimated at 26.0–28.3 million kg for the Florida Gulf shrimp fishery. With the finfish-to-shrimp ratio of of 2.8:1 for the South Atlantic fishery and the current landings information for Florida, the finfish bycatch for the Florida Atlantic shrimp fishery can be estimated at 5.0 million kg. Since 1990, considerable research has been conducted to characterize bycatch composition and to develop methods to reduce bycatch in the Gulf and the South Atlantic shrimp fisheries (Nance, 1992, 1993; GSAFDF[2,3]; Nichols et al.[4]; NMFS[5]). In addition, numerous fishery-independent surveys examining bycatch characterization and the efficiency of bycatch reduction devices (BRDs) have been conducted by state and private organizations throughout the southeastern U.S.A. (Burrage et al.[6]).

In 1990, the Florida Marine Fisheries Commission (FMFC; now Florida Fish and Wildlife Conservation Commission) began to develop a shrimp fishery management plan that included a mandate to reduce the bycatch of total finfish biomass in shrimp trawls by 50%. Responding to this policy decision, a bycatch-characterization study of the inshore Florida shrimp fishery was conducted statewide (Coleman et al.[7]; Coleman et al.[8]). Field studies comparing the efficiencies of two types of BRDs (Florida fish eye [FFE], large-mesh extended-mesh funnel [EMF]) in otter trawls and rollerframe trawls were also conducted (Continental Shelf Associates Inc.[9]; Coleman and Koenig[10]; Coleman et al.[11]).

The issue of bycatch in the Florida shrimp trawl fishery has exacerbated conflicts between conservationists and recreational and commercial fishermen over the allocation of marine resources. Relevant issues include the following: 1) the high mortality rates of economically important juvenile finfish caught in shrimp trawls, which could reduce harvestable finfish stocks; 2) the high mortality rates of nonharvested species caught in shrimp trawls, which could alter the overall health of the marine environment; and 3) the perceived waste of bycatch species that are discarded.

This controversy was partly responsible for the passage of a Florida constitutional amendment (Article X, Section 16) that reduced the size of shrimp trawl nets used in the coastal shrimp fishery to 500 sq. ft. (45 m^2) of mesh area per net and limited the number of nets to two per vessel. In previous studies conducted in Florida to examine the efficiency of BRDs in shrimp trawls (Coleman and Koenig[10]), net sizes greatly exceeding that authorized by the amendment were tested. The goal of our study was to test how efficiently the FFE and EMF excluded finfish in small otter trawls (overall mesh area=45 m^2) of various mouth-perimeter sizes. This information can be used by fisheries managers when considering the use of BRDs in inshore and nearshore shrimp fisheries.

Materials and methods

Tampa Bay is located on the west-central coast of Florida (Fig. 1) and is the largest open-water estuary in the state (Lewis and Estevez, 1988). The bay is a subtropical estuary that has patches of fringing seagrass meadows (Lewis et al., 1981), but fine sand is the predominant seabottom type (Brooks[12]).

Gear specifications

Conventional semiballoon otter trawls (Fig. 2) are used to harvest pink shrimp (*Farfantepenaeus duorarum*) in Tampa Bay. Otter trawls are typically used on unvegetated, sandy-bottom areas. We tested the effectiveness of

[3] GSAFDF (Gulf and South Atlantic Fisheries Development Foundation). 1993. Organization and management of a Gulf of Mexico and south Atlantic Ocean fishery bycatch management program (year 2). Final report to National Marine Fisheries Service (award NA37FD0032). GSAFDF, Suite 997, Lincoln Center, 5401 West Kennedy Boulevard, Tampa, FL 33609, 65 p.

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[5] NMFS (National Marine Fisheries Service). 1995. Cooperative research program addressing finfish bycatch in the Gulf on Mexico and south Atlantic shrimp fisheries: a report to Congress. National Marine Fisheries Service, Southeast Fisheries Center, Southeast Regional Office, 9721 Executive Center Drive, St. Petersburg FL 33702, 68 p.

[6] Burrage, D. D., S. G. Branstetter, G. Graham, and R. K. Wallace. 1997. Development and implementation of fisheries bycatch monitoring programs in the Gulf of Mexico. Report to the U. S. Environmental Protection Agency (report MX-994717-95-0). Mississippi State University, P.O. Box 5325, Mississippi State, MS 39762, 103 p.

[7] Coleman, F. C., C. C. Koenig, and W. F. Herrnkind. 1991. Survey of the Florida inshore shrimp trawling bycatch and preliminary tests of bycatch reduction devices. First annual report to the Florida Department of Natural Resources. National Marine Fisheries Service MARFIN grant NA37FF0051. Institute for Fishery Resource Ecology, Florida State Univ., Tallahassee, FL 32306, 25 p.

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[9] Continental Shelf Associates, Inc. 1992. Commercial food shrimp fishery impacts on by-catch in the lower St. Johns River, Florida. Draft final report C-7238. Continental Shelf Associates, Inc., 759 Parkway Street, Jupiter, FL 33477, 35 p.

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[11] Coleman, F. C., P. Steele, and W. Teehan. 1996. Use of bycatch reduction devices in small trawls of sizes set by the net ban. Final Report. Florida Department of Environmental Protection contract MR081. Florida Dep. Environ. Protection, 100 8th Avenue S.E., St. Petersburg, FL 33701, 75 p.

[12] Brooks, H. K. 1974. Geological oceanography. *In* Summary of knowledge, eastern Gulf of Mexico (J. I Jones, R. R Ring, M. O. Rinkel, and R. E. Smith, eds.), p. IIE1-50. Fla. State Univ. Syst. Inst. Oceanogr., St. Petersburg, FL.

two BRDs, the FFE and the EMF (Fig. 3) in three sizes of otter trawls in Tampa Bay during October–December 1996 (fall) and February–April 1997 (winter). Both BRDs are standard devices that have been recommended by NMFS, are used by the commercial fishing sector, and have been extensively tested in offshore and inshore waters throughout the southeastern United States (Murray et al., 1992; Watson et al., 1993; Rogers et al., 1997; Coleman et al.[7] Christian et al.[13]; McKenna and Monaghan[14]).

The otter trawl dimensions were as follows: 1) 14-m net: mouth circumference = 14.0 m, float-line length = 6.3 m, lead-line length = 6.9 m; 2) 17-m net: mouth circumference = 17.0 m, float-line length = 6.9 m, lead-line length = 7.8 m; 3) 20-m net: mouth circumference = 20.0 m, float-line length = 8.1 m, lead-line length = 9.4 m. The nets were of appropriate lengths to conform to the 45-m^2 total-mesh-area rule. Net perimeters were chosen after consultation with commercial shrimpers and personnel from the NMFS Laboratory Harvesting Section, Pascagoula, Mississippi. All net bodies were constructed of no. 9 twine and had a stretch-mesh size of 3.8 cm; the tailbag was constructed of no. 18 twine and had a stretch-mesh size of 3.2 cm. The FFE was constructed of 13-mm-diameter stainless steel rods. It had an overall length of 30 cm and a 15-cm × 15-cm opening to allow fish to escape. The FFE was mounted at the top center of the tailbag at 70% of the distance between the tie-off rings and the beginning of the codend (Watson et al., 1993; Christian et al.[13]), creating an area of reduced water flow directly behind the FFE, which would allow fish to escape. The EMF had an overall length of 121 cm and a circumference of 120 meshes; it consisted of a web funnel (3.5-cm stretch-mesh size) surrounded by a larger-mesh "escape" section (21-cm stretch-mesh size) held open by a plastic-coated hoop. One side of the funnel was extended to form a lead panel that created an area of reduced water flow on the back side of the funnel, similar to that created by the FFE.

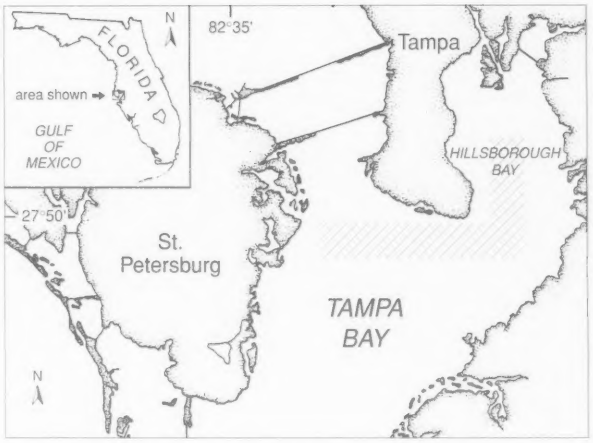

Figure 1

Tampa Bay, Florida. Hatched region shows sampling area.

To conform to federal regulations, each net was equipped with a turtle excluder device (TED) placed near the mouth of the tailbag (Fig. 2). The standard super-shooter TED consisted of a metal grid of seven aluminum bars with a 9-cm interbar distance; the grid was set at a 45° angle to direct turtles downward toward the escape opening (Watson et al., 1993). Sewn in front of the TED was a section of webbing (3.2-cm stretch-mesh) that formed an accelerator funnel (Fig. 3A), which increased the velocity of water and entrained organisms both through the TED and into the net tailbag. The tailbag section and the combined TED and accelerator-funnel section could be zipped to any trawl body, regardless of size. The zipper ensured random pairing of trawl body and tailbag and enabled the experimental and control nets to be easily exchanged throughout the project. The BRDs and TEDs used during this project were approved by the NMFS Laboratory Harvesting Section, Pascagoula, Mississippi.

Both types of BRDs were tested in each net size. For each net size, one net of a matched pair was equipped with either the FFE or the EMF and served as the experimental net and the other, unaltered net served as the control. In the experimental net, the FFE or EMF was installed behind the TED-accelerator funnel section. The net with the BRD was deployed off a randomly chosen side of the boat and its paired control net was deployed simultaneously off the other side in a double-rig trawl towed from 3.5-m outriggers. Each net was spread by two 123-cm × 62-cm wooden trawl doors linked by a tickler chain.

[13] Christian, P. A., D. L. Harrington, D. R. Amos, R. G. Overman, L. G. Parker, and J. B. Rivers. 1993. Final report on the reduction of finfish capture in south Atlantic shrimp trawls. Final report to National Marine Fisheries Service (award NA27FD 0070-01). Univ. Georgia, 715 Bay Street, Brunswick, GA 31520, 83 p.

[14] McKenna, S. A., and J. P Monaghan Jr. 1993. Gear development to reduce bycatch in the North Carolina trawl fisheries. Completion report to Gulf and South Atlantic Fisheries Development Foundation (cooperative agreement NA90AA-H-SK052). North Carolina Div. Mar. Fish., 3441 Arendell Street,Morehead City, NC 28557, 79 p.

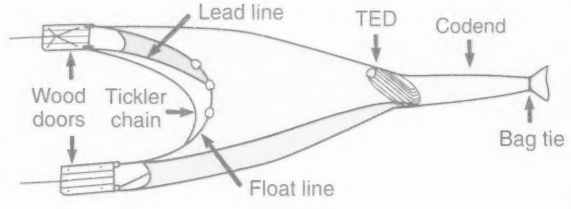

Figure 2

Components of a semiballoon otter trawl equipped with a super shooter turtle excluder device (TED). The TED is required in all shrimp nets in Florida.

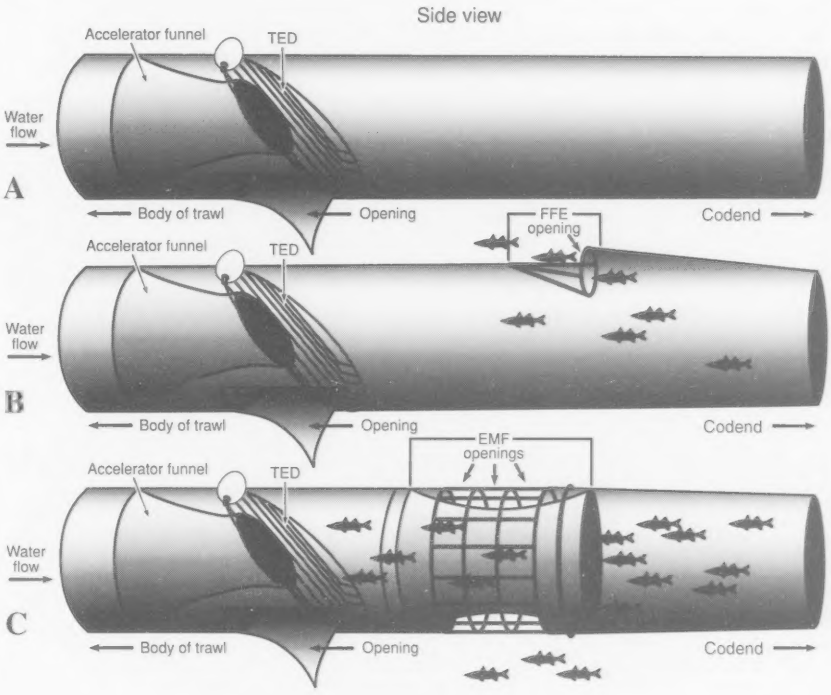

Figure 3

Stylistic diagram of the bycatch reduction devices used in this study: (**A**) Control net equipped with an accelerator funnel in front of the TED; (**B**) net with Florida fisheye (FFE), the device is inserted into the tailbag behind the TED; (**C**) net with large-mesh extended-mesh funnel (EMF) inserted directly behind the TED.

Sampling protocol

Our sampling protocol was established in consultation with representatives from the NMFS Pascagoula Laboratory and the FMFC. Coleman and Koenig[9] established that TEDs did not work as finfish excluder devices in inshore waters; therefore we did not test their exclusion efficiencies.

Sampling was conducted aboard a 35-ft, diesel-powered, Bruno & Stillman trawler boat, modified with outriggers. The nets were deployed and retrieved with a hydraulic powered system. Prior to installing and testing the BRDs, we equipped all pairs of nets of each size with the combined TED and accelerator-funnel sections and tested them for comparable catchability.

To test each BRD type in each size of net, we conducted twenty paired tows at night during a three-week sampling period in each season. Each pair of nets was towed 10 times within a two-week time period. To minimize any potential bias inherent to a particular net or side of the boat, the two nets of each pair were switched to opposite sides of the boat after 10 tows were completed. All paired nets were towed in water depths of 3.5 to 5.0 m for 30-min bottom time at an average speed of 2.5 kn; speed was determined through use of the global positioning system (GPS). All trawling was conducted in areas where the commercial shrimp fishery operates.

The catches from the paired nets (BRD and control) were maintained separately and were sorted onboard the vessel. After each tow, the shrimp, finfish, invertebrates (horseshoe crabs, portunid crabs, sponges, tunicates) and "trash" (seagrass, rocks, shells, anthropogenic debris, etc.) from each net were separated. The large invertebrates (horseshoe crabs, blue crabs, etc.) and trash were weighed separately, the invertebrates were counted, and both the invertebrates and the trash were discarded. The total catch of shrimp and finfish from each net was weighed separately. The shrimp were counted, sex was determined for 10 randomly chosen individuals, and their carapace lengths (CL) were measured to the nearest 0.1 mm. These measurements from the 20 replicate tows were combined to obtain length-frequency distributions for the shrimp. The remaining bycatch, composed of finfish and small invertebrates, was weighed. If the total weight of the bycatch was less than or equal to 4.5 kg, the entire sample was kept; if the weight of the sample exceeded 4.5 kg, a subsample weighing a total of 4.5 kg + 20% of the total bycatch weight was kept. All species of vertebrates and in-

vertebrates from each bycatch sample or subsample were identified; finfish that could not be identified onboard were labeled and returned to the laboratory for identification. All individuals of each finfish species were counted and the finfish bycatch sample or subsample was weighed. To obtain an estimate of the size-frequency distribution for each species of finfish, we measured the standard length (SL) to the nearest 1 mm of 20 randomly selected individuals of each species from each tow and combined the measurements from the 20 replicate tows. If fewer than 20 individuals were caught in a tow, all individuals captured in that tow were measured.

All weights were standardized to grams per minute towed to estimate CPUE (biomass). All counts of individual species were standardized to number per minute towed (NPUE).

Statistical analyses

Statistical analyses followed Sokal and Rohlf (1995). Parametric statistics were applied when the data conformed to the parametric assumptions of normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test). Variables that did not conform to parametric assumptions were transformed to log (biomass or number)+1. Nonparametric statistics were employed only after appropriate methods were deemed unsuccessful in transforming the data to meet parametric assumptions. Both parametric and nonparametric statistical analyses were completed by using the STATISTICA software package (Statsoft Inc, 1999). Using *t*-tests, we evaluated the performance of the paired nets prior to the addition of the BRDs and compared the catchability of the BRD-equipped net to its control. Because we used a paired-tow design for field testing, we analyzed each net size and type of BRD separately; net sizes and BRDs were not directly compared with each other but were always compared with the controls. The ability of a BRD-equipped trawl to retain shrimp while reducing bycatch was assessed by comparing the CPUE (biomass) and NPUE of finfish and shrimp and by comparing the CPUE and the NPUE of the 10 most abundant finfish species in the BRD-equipped net with CPUE and NPUE data for its paired control net. The CPUE and NPUE of shrimp caught, calculated as described above, were based on actual weight and numbers of shrimp caught in each trawl. When the bycatch was subsampled, the finfish biomass or number was estimated using the formula

$$\textit{Finfish biomass or number} = \frac{\textit{Finfish subsample CPUE or NPUE} \times \textit{Total bycatch weight}}{\textit{Subsample weight}}.$$

Because our sampling period ranged over two seasons, we considered the interactive effects of season and net type (BRD-equipped or control) for each net size by using analysis of variance (ANOVA). We then used the least-squares difference (LSD) *post hoc* test to locate the significant differences. Differences between the net with the BRD and its paired control net in the size-frequency distribution of the 10 most abundant fish species were assessed by using the Kolmogorov-Smirnov two-sample test. To determine the percent reduction or increase in the biomass and number of each of the top ten finfish species, we compared the BRD-equipped nets with the control nets by using the untransformed mean CPUE and NPUE data for shrimp and finfish and the total number of individuals subsampled. Percent reduction for either CPUE or NPUE was then calculated (from Rogers et al., 1997) as

$$\textit{Percent difference} = \frac{(\textit{CPUE or NPUE of BRD net} - \textit{CPUE or NPUE of control net}) \times 100}{\textit{CPUE or NPUE of control net}}.$$

Results

No significant differences were found in total weight of the finfish or shrimp catch between nets of equal size prior to the addition of the BRDs. Similarly, the total weight of finfish or shrimp was not significantly affected by trawl position. The standardized mean ratio of finfish bycatch to shrimp biomass for all control net sizes combined was 5.3:1 (range 2.9:1–11.3:1). The standardized mean ratio for the BRD-equipped nets (3.8:1; range 2.5:1–4.9:1) was not significantly different but was substantially lower than that of the control nets.

CPUE and NPUE

In contrast to results with the control nets, there were no significant differences in either biomass or number of shrimp captured in the 17-m net or the 20-m net equipped with either BRD (Table 1). In winter, the biomass and the number of shrimp captured in the 14-m net equipped with either BRD were significantly lower than these quantities captured in the corresponding control net (FFE: P=0.025; EMF: P=0.008). On the contrary, both the biomass and number of finfish were significantly and notably lower in most of the BRD-equipped nets than they were in the control nets (for significant differences, P range for the FFE= 0.025–0.001 and P range for the EMF= 0.027–<0.001). The only exception was in the number of finfish caught in winter by nets equipped with either BRD.

Significant seasonal differences always occurred in shrimp CPUE (FFE: P<0.001 for all tests; EMF P range: 0.003–<0.001) and nearly always occurred in shrimp NPUE (FFE P range: 0.003–<0.001; EMF P range: 0.002–0.001; exception: NPUE for the 17-m EMF-equipped net) and accounted for most of the variation in CPUE observed for each net size. Nearly all significant differences in shrimp CPUE and NPUE between seasons were due to a larger catch of shrimp in winter. The only significant interactive

Table 1

Comparison of percentage differences in shrimp and finfish biomass (CPUE) and number (NPUE) from the 14-m, 17-m, and 20-m nets equipped with the Florida fisheye (FFE) and extended mesh funnel (EMF) bycatch reduction devices (BRDs). CPUE is the mean weight (grams) caught per minute towed, and NPUE is the mean number of individuals caught per minute towed. Significance levels of ≤0.05 are denoted by asterisks.

		Shrimp						Fish					
		CPUE			NPUE			CPUE			NPUE		
		BRD	control	% diff.	BRD	control	% diff.	BRD	control	% diff.	BRD	control	% diff.
FFE													
Fall 1996	14-m net	29	31	−6	2	2	−5	99	154	−35*	3	4	−34*
	17-m net	21	21	4	2	1	7	70	105	−33*	2	3	−41*
	20-m net	17	16	6	1	1	11	176	196	−11	3	5	−39
Winter 1997	14-m net	36	45	−20*	2	2	−16*	113	132	−14	4	4	3
	17-m net	55	59	−6	4	4	−5	119	124	−4	12	12	5
	20-m net	42	38	11	2	2	14	114	130	−12	7	6	28
EMF													
Fall 1996	14-m net	32	33	−5	2	2	−5	90	168	−46*	3	5	−39*
	17-m net	23	25	−9	2	2	−11	60	151	−60*	2	4	−60*
	20-m net	12	12	0	1	1	0	116	174	−33*	3	5	−28*
Winter 1997	14-m net	42	60	−29*	2	3	−25*	106	130	−18	7	6	28
	17-m net	31	39	−18	2	2	−21	86	121	−28*	8	7	7
	20-m net	25	22	18	1	1	17	133	169	−21	5	4	12

effect between season and BRD type occurred in shrimp CPUE for the 14-m, EMF-equipped net (P=0.027).

Similarly, finfish CPUE differed seasonally for most net sizes (FFE P range: 0.009–< 0.001; EMF P for all tests: <0.001; exceptions: 14-m and 17-m, EMF-equipped nets), and NPUE differed seasonally for all net sizes (FFE P for all tests: <0.001; EMF P range: <0.001–0.000). However, the season in which the largest catch was harvested differed between net sizes and between BRD types. Both finfish CPUE and NPUE were significantly higher during winter than during fall in the 14-m and 17-m FFE-equipped nets but finfish CPUE and NPUE were significantly lower during fall than during winter in the 20-m FFE-equipped net. For the EMF-equipped nets, finfish CPUE differed seasonally only in the 20-m nets; CPUE in winter was higher than in fall. Finfish NPUE values for the EMF-equipped nets were always significantly higher in winter (P for all tests: <0.001).

Percent reduction

Differences in the percentage of shrimp in the BRD-equipped versus the control nets varied with season, net size, and BRD type. Although many of these differences were not significant (Table 1), patterns in shrimp loss or retention were apparent. Other than the 17-m, FFE-equipped net in fall, the addition of a BRD to a 14-m or 17-m net resulted in a reduction in shrimp CPUE and NPUE, regardless of BRD type. However, the reductions were significant only for the 14-m nets in winter. In contrast, shrimp CPUE and NPUE usually were slightly higher in the 20-m BRD-equipped nets than in the control nets.

Finfish CPUE was always less in BRD-equipped nets than in control nets (Table 1). The reduction in finfish bycatch CPUE was nearly always significant in fall, and most reductions were dramatic (20–60%). Reductions in finfish NPUE also had a strong seasonal component. For all net sizes, finfish bycatch NPUE in the BRD-equipped nets was notably (and nearly always significantly) less than that in the control nets in fall, whereas more (but not significantly more) finfish were captured in the BRD-equipped nets than in the control nets in winter.

Catch composition

Most of the biomass in both the BRD-equipped and the control nets usually was composed of finfish (30–70%). The remainder of the catch consisted of shrimp (15–20%), horseshoe crabs (*Limulus polyphemus*) and blue crabs (*Callinectes sapidus*) (15–58%), and miscellaneous invertebrates such as ctenophores, portunid crabs, sponges, and gastropods (<25%). When the catch of arthropods (principally horseshoe crabs) was large, the finfish catch was generally small. The shrimp catch was relatively stable even when the bycatch composition fluctuated.

Horseshoe crabs were the most abundant invertebrate bycatch species. A total of 2867 horseshoe crabs were caught during the two sampling seasons; largest catches occurred during fall. Although the catch of horseshoe crabs caught in the BRD-equipped nets was generally smaller

than the catch in the corresponding control nets, only in the 14-m FFE-equipped net and the 20-m EMF-equipped net was the number of horseshoe crabs caught significantly lower than the number of horseshoe crabs caught in the corresponding control nets (P=0.001 and P=0.05, respectively). Blue crabs were the second most abundant invertebrate bycatch species. A total of 544 blue crabs were caught during the two sampling seasons; the largest catches occurred during winter. Although fewer blue crabs were caught in the BRD-equipped nets, only in the 14-m EMF-equipped net was the number of blue crabs significantly lower than that in the corresponding control net (P=0.005 for both seasons).

A total of 44 species of finfish were caught during our study (Table 2). Numerically, ten finfish species composed more than 92% of the total finfish count, and a single species, the leopard searobin (*Prionotus scitulus*), composed over 40%. Abundance differed greatly between seasons for nearly all fishes (Table 2). The silver jenny (*Eucinostomus gula*), hardhead catfish (*Arius felis*), gafftopsail catfish (*Bagre marinus*), sand seatrout (*Cynoscion arenarius*), and silver perch (*Bairdiella chrysoura*) predominated in the catch during fall. These were replaced during winter by the leopard searobin (*Prionotus scitulus*), blackcheek tonguefish (*Symphurus plagiusa*), southern kingfish (*Menticirrhus americanus*), pinfish (*Lagodon rhomboides*), and spadefish (*Chaetodipterus faber*).

Ten of the finfish species that we captured are important to the recreational or commercial fishing sectors. These are the southern kingfish (*Menticirrhus americanus*), scaled sardine (*Harengula jaguana*), striped anchovy (*Anchoa hepsetus*), bay anchovy (*Anchoa mitchelli*), spot (*Leiostomus xanthurus*), spotted seatrout (*Cynoscion nebulosus*), gulf menhaden (*Brevoortia patronus*), gulf flounder (*Paralichthys albigutta*), pompano (*Trachinotus carolinus*), and permit (*Trachinotus falcatus*). These species each accounted for less than 1% of the total finfish count, except for the southern kingfish, which accounted for 4.6%.

For the species captured principally in fall, the overall proportion of the bycatch excluded by the 14-m and 17-m BRD-equipped nets was similar, and both sizes of nets tended to exclude high percentages of these fishes (Fig. 4). The 20-m BRD-equipped net was not as effective in reducing the numbers of these species. For the species captured principally in winter, the efficiency with which the BRD-equipped nets excluded these fishes varied among net sizes and BRD types. For some species (e.g. the leopard searobin and blackcheek tonguefish), BRD-equipped nets retained more individuals than did the corresponding control nets.

Size distribution

Shrimp size-frequency distributions for pooled trawls (BRD-equipped net and its corresponding control) had significant seasonal variation (P<0.001, t=16.1, df=2,416). In fall, mean carapace length was 23.4 mm (SD=4.7 mm) and the range was 11.2–40.4 mm, whereas in winter, the mean was 27.0 mm (SD=6.5 mm) and the range was 7.3–43.8 mm.

Mean sizes of the 10 most abundant finfish species differed significantly between the BRD-equipped nets and their corresponding controls in approximately 25% of the trawls with the FFE-equipped nets and in 30% of the trawls with the EMF-equipped nets (Table 3). The differences in mean sizes of individuals were usually small regardless of statistical significance. Nevertheless, the ratio of comparisons in which mean size of fish from BRD-equipped nets was smaller than that of fish from control nets to comparisons in which the mean size of fish from BRD-equipped nets was larger than that of fish from control nets was 2:1 for the trawls with the FFE-equipped net and 3:1 for the trawls with the EMF-equipped net. The only net size and BRD-type combination for which the mean size of individuals from the BRD-equipped net was always smaller than that from the control net was the 14-m FFE-equipped net.

Discussion

Shrimp catch

Although most BRD-equipped nets retained less biomass and fewer numbers of shrimp than did their corresponding control nets, the difference in these measures between the BRD-equipped nets and their controls was significant only for the 14-m net in winter. Indeed, shrimp biomass and number in the 20-m BRD-equipped net slightly exceeded biomass and number in the corresponding control net. In previous studies, researchers evaluating the efficiency of BRDs also found that the shrimp catch in BRD-equipped nets tended to be higher than in control nets. They attributed the increase in shrimp catch in their BRD-equipped net to a greater net spread caused by a reduction in the amounts of bycatch and drag (Rogers et al., 1997; Coleman and Koenig[10]) and to an increase in the volume of water filtered through the net due to the position of the BRD (Christian et al.[13]).

The numbers of shrimp retained in all BRD-equipped nets and in nearly all control nets were greater in winter than in fall. In the Tampa Bay region, adult female shrimp migrate out of the bay to spawn during spring and fall and juvenile shrimp are recruited into the bay during summer and winter (Eldred et al., 1965). The increase in abundance and the larger size range of shrimp that we caught during winter support this finding.

Finfish bycatch

Overall, both BRDs proved to be highly effective in reducing finfish bycatch without greatly reducing shrimp catch. The reduction in bycatch was usually significant in the 14-m and 17-m BRD-equipped nets. The mean ratio of finfish biomass to shrimp biomass in our BRD-equipped nets was within the range of ratios reported by others who tested the BRD-equipped nets in the Gulf (Alverson et al., 1994; GSAFDF[2]). Branstetter (1997) and Watson et al.[15]

[15] Watson, J., A. Shah, and D. Foster. 1997. Report on the status of bycatch reduction device (BRD) development. National Marine Fisheries Service, Mississippi Laboratories, P.O. Drawer 1207, Pascagoula, MS, 39568.

Table 2

Percentage contribution of individual finfish species subsampled from catches of otter trawls towed in Tampa Bay during fall 1996 and winter 1997. All tows have been pooled and incorporate both BRD-equipped and control nets for all three trawl-net sizes. Seasonal percentages are calculated for each species.

Common name	Species	Total number of sampled fish	% (Total)	% (Fall)	% (Winter)
Leopard searobin	*Prionotus scitulus*	28,299	41.02	6.6	93.4
Silver jenny	*Eucinostomus gula*	9134	13.24	86.2	13.8
Gafftopsail catfish	*Bagre marinus*	6658	9.65	83.5	16.5
Blackcheek tonguefish	*Symphurus plagiusa*	4613	6.69	35.6	64.4
Sand seatrout	*Cynoscion arenarius*	3365	4.88	80.6	19.4
Southern kingfish	*Menticirrhus americanus*	3193	4.63	44.0	56.0
Hardhead catfish	*Arius felis*	2949	4.27	88.0	12.0
Silver perch	*Bairdiella chrysoura*	2463	3.57	64.1	35.9
Pinfish	*Lagodon rhomboides*	1503	2.18	0.8	99.2
Spadefish	*Chaetodipterus faber*	1487	2.16	10.7	89.3
Bighead searobin	*Prionotus tribulus*	759	1.10	12.9	87.1
Scaled sardine	*Harengula jaguana*	642	0.93	59.4	40.6
Hogchocker	*Trinectes maculatus*	538	0.78	37.7	62.3
Striped anchovy	*Anchoa hepsetus*	524	0.76	25.5	74.5
Southern puffer	*Sphoeroides nephelus*	346	0.50	5.2	94.8
Southern hake	*Urophycis floridana*	337	0.49	0.0	100.0
Bay anchovy	*Anchoa mitchelli*	320	0.46	1.3	88.7
Pigfish	*Orthopristis chrysoptera*	274	0.40	3.7	96.3
Inshore lizardfish	*Synodus foetens*	237	0.34	76.4	23.6
Lined sole	*Achirus lineatus*	160	0.23	26.8	73.2
Lookdown	*Selene vomer*	138	0.20	100.0	0.0
Atlantic bumper	*Chloroscombrus chysurus*	135	0.20	97.7	2.3
Striped burrfish	*Chilomycterus schoepfi*	128	0.19	2.3	97.7
Ocellated flounder	*Ancylopsetta quadrocellata*	93	0.13	1.1	98.9
Spot	*Leiostomus xanthurus*	89	0.13	0.0	100.0
Crested blenny	*Hypleurochilus geminatus*	82	0.12	1.2	98.8
Rough silverside	*Membras martinica*	78	0.11	24.4	75.6
Planehead filefish	*Monacanthus hispidus*	76	0.11	15.7	84.3
Threadfin herring	*Opisthonema oglinum*	72	0.10	38.8	61.2
Scrawled cowfish	*Lactophrys quadricornis*	64	0.09	3.2	96.8
Crevalle jack	*Caranx hippos*	47	0.07	100.0	0.0
Sheepshead	*Archosargus probatocephalus*	46	0.07	97.8	2.2
Spotted seatrout	*Cynoscion nebulosus*	43	0.06	100.0	0.0
Orange filefish	*Aluterus schoepfi*	22	0.03	9.1	90.9
Gulf menhaden	*Brevoortia patronus*	19	0.03	68.4	31.6
Gulf toadfish	*Opsanus beta*	15	0.02	13.4	86.6
Harvestfish	*Peprilus alepidotus*	10	0.01	50.0	50.0
Leatherjacket	*Oligoplites saurus*	6	0.01	100.0	0.0
Shrimp eel	*Ophichthus gomesi*	5	0.01	80.0	20.0
Gulf flounder	*Paralichthys albigutta*	5	0.01	40.0	60.0
Gulf butterfish	*Peprilus burti*	4	0.01	50.0	50.0
Striped mojarra	*Diapterus plumieri*	1	0.00	100.0	0.0
Pompano	*Trachinotus carolinus*	1	0.00	100.0	0.0
Permit	*Trachinotus falcatus*	1	0.00	100.0	0.0

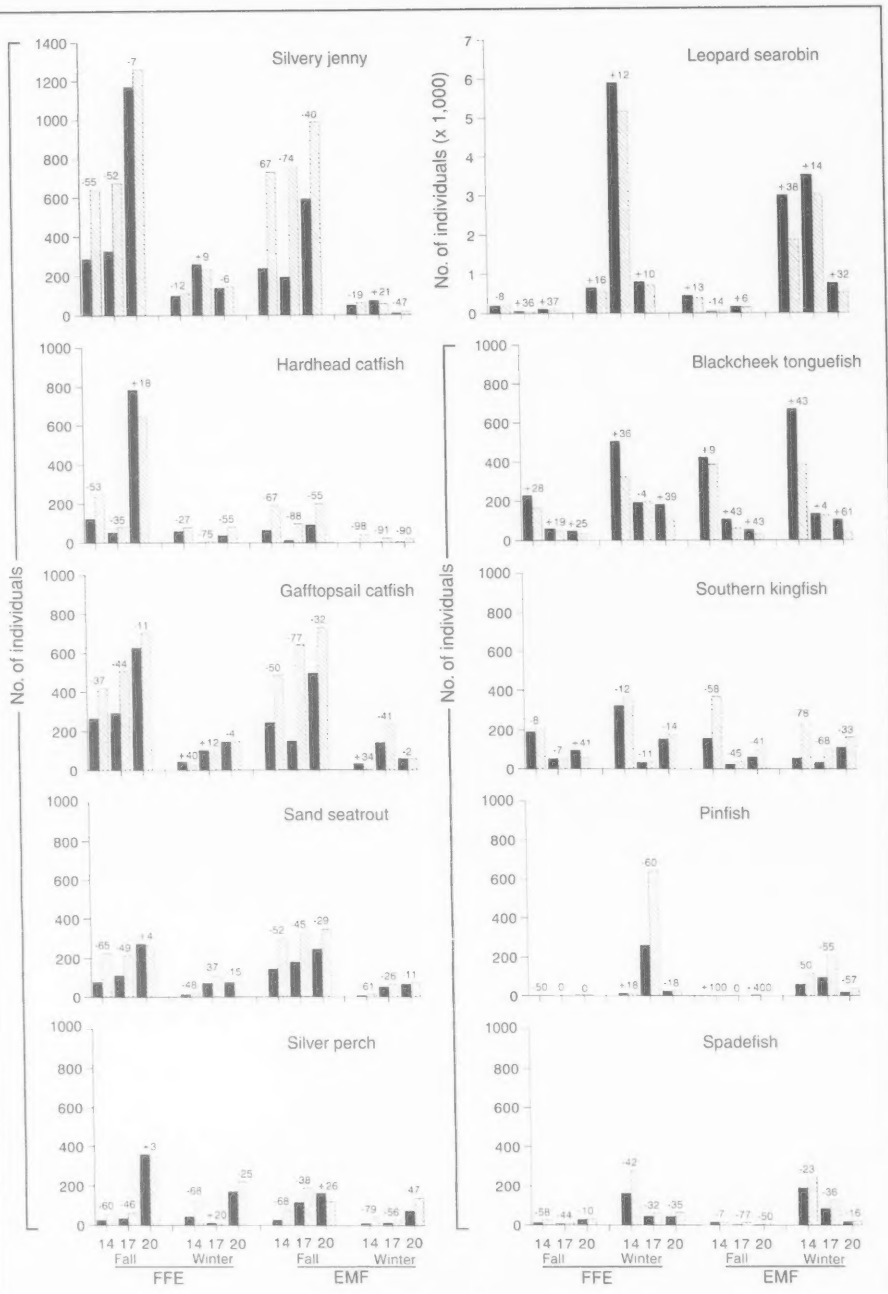

Figure 4

Comparisons of species-specific seasonal catch and retention rates for the 10 finfish species most commonly captured in the three sizes of period bycatch reduction device (BRD)-equipped nets (black bars) and control shrimp-trawl nets (hatched bars). Each vertical bar represents the total number of fish captured in 20 tows. Numbers over pairs of bars are the percent losses or gains in numbers of individuals captured by the BRD-equipped net versus the paired control net. FFE = Florida fisheye BRD; EMF = extended mesh funnel BRD. Column 1 shows species captured principally in fall; column 2 shows species captured principally in winter.

Table 3

Comparison of mean standard length measurements (mm) of the most abundant species caught in nets equipped with either the Florida fisheye (FFE) or the extended mesh funnel (EMF) bycatch reduction device (BRD) and their corresponding control nets. The three nets of different sizes used are denoted by the measurements of their perimeters: 14 m, 17 m, and 20 m. Significance levels are ≤0.05(*). Values represent mean and standard deviation, and sample sizes (n) are shown in parentheses. Dashes indicate that no fish were captured.

		Fall			Winter		
		14 m	17 m	20 m	14 m	17 m	20 m
Common name	Treatment	Mean, SD (n)	Mean, SD (n)	Mean, SD (n)	Mean, SD (n)	Mean, SD (n)	Mean, SD (n)
Florida fisheye bycatch reduction device							
Leopard searobin	BRD	103, 26 (191)	83, 13 (47)	98, 22 (85)	94*, 22 (327)	78, 17 (400)	97, 17 (309)
	Control	108, 24 (204)	90, 26 (30)	100, 22 (63)	96, 19 (317)	77, 13 (400)	97, 16 (325)
Silver jenny	BRD	66*, 09 (259)	75, 14 (286)	76, 08 (340)	82*, 07 (99)	73, 09 (180)	86, 07 (123)
	Control	69, 09 (394)	75, 10 (371)	76, 08 (339)	84, 09 (113)	82, 09 (189)	88, 12 (136)
Gafftopsail catfish	BRD	123*, 10 (203)	134, 13 (267)	124*, 10 (317)	143, 30 (43)	154, 26 (103)	147, 19 (131)
	Control	132, 10 (302)	131, 08 (347)	123, 16 (326)	136, 11 (26)	152, 23 (88)	147, 17 (140)
Blackcheek tonguefish	BRD	115*, 16 (214)	123, 20 (58)	121, 20 (48)	117, 15 (374)	155, 16 (185)	115*, 16 (160)
	Control	119, 16 (154)	125, 18 (47)	122, 19 (36)	120, 18 (293)	115, 18 (180)	119, 16 (111)
Sand seatrout	BRD	135*, 29 (78)	150*, 30 (110)	150, 33 (226)	177, 30 (12)	167, 29 (71)	174*, 22 (71)
	Control	146, 29 (217)	157, 26 (213)	155, 30 (225)	159, 27 (23)	169, 18 (71)	181, 30 (88)
Southern kingfish	BRD	137, 34 (185)	158, 14 (50)	135, 33 (93)	154*, 22 (275)	149, 33 (31)	170*, 21 (146)
	Control	138, 34 (202)	143, 35 (54)	136, 34 (55)	153, 24 (311)	142, 33 (35)	164, 20 (171)
Hardhead catfish	BRD	94*, 30 (120)	109, 48 (54)	94, 29 (325)	196, 88 (58)	180, 127 (2)	158, 79 (34)
	Control	101, 37 (224)	99, 32 (80)	99, 41 (304)	206, 80 (79)	199, 66 (8)	173, 73 (83)
Silver perch	BRD	88, 16 (23)	84, 17 (33)	89, 15 (224)	114, 11 (42)	94, 05 (10)	108, 07 (162)
	Control	90, 10 (58)	92, 17 (61)	89, 14 (235)	110, 11 (131)	97, 15 (9)	109, 11 (224)
Pinfish	BRD	90 (1)	—	86, 23 (2)	93, 17 (11)	79, 07 (159)	84, 14 (23)
	Control	103, < 1 (2)	—	97, 23 (2)	96, 11 (9)	78, 06 (194)	84, 13 (27)

continued

investigated the effectiveness of BRD designs that were similar to ours in offshore waters of the Gulf and the south Atlantic. They reported reductions in finfish biomass of 4–46% for the FFE and 18–35% for the EMF and respective reductions in shrimp biomass of 0–16% and 0–4%.

Our biomass reduction ratios of finfish to shrimp ranged broadly and unpredictably among net sizes and between BRD types and seasons, and our percentages of change in both biomass and numbers of finfish ranged widely between the BRD-equipped nets and their corresponding controls. In our study, the proportion of finfish to invertebrates and the species compositions and size distributions of these two groups influenced the ratio of finfish to shrimp. Bycatch reduction and shrimp retention have also

Table 3 (continued)

		Fall			Winter		
		14 m	17 m	20 m	14 m	17 m	20 m
Common name	Treatment	Mean, SD (*n*)	Mean, SD (*n*)	Mean, SD (*n*)	Mean, SD (*n*)	Mean, SD (*n*)	Mean, SD (*n*)
Extended mesh funnel bycatch reduction device							
Leopard searobin	BRD	104, 23 (317)	80, 26 (43)	99, 21 (110)	91, 22 (391)	86, 20 (359)	101, 14 (155)
	Control	108, 19 (310)	92, 26 (50)	95, 22 (121)	91, 21 (383)	85, 19 (359)	100, 15 (152)
Silver jenny	BRD	67*, 09 (217)	76*, 09 (187)	74, 09 (360)	81, 07 (51)	76*, 07 (70)	87, 08 (10)
	Control	70, 09 (379)	78, 09 (381)	74, 08 (375)	80, 09 (62)	82, 12 (58)	95, 12 (19)
Gafftopsail catfish	BRD	129*, 12 (167)	132*, 12 (119)	125*, 18 (309)	147, 28 (32)	139*, 19 (139)	149, 19 (57)
	Control	124, 09 (343)	129, 19 (385)	121, 10 (394)	137, 15 (21)	148, 33 (185)	154, 17 (58)
Blackcheek tonguefish	BRD	115*, 15 (315)	126, 19 (107)	124, 18 (45)	122, 18 (346)	111, 20 (134)	114, 17 (99)
	Control	118, 16 (318)	129, 23 (61)	124, 17 (31)	122, 18 (273)	117, 19 (127)	117, 15 (41)
Sand seatrout	BRD	141*, 24 (144)	142, 29 (179)	145, 31 (227)	163, 37 (5)	159, 34 (51)	154*, 50 (57)
	Control	149, 32 (274)	146, 31 (289)	147, 28 (328)	144, 52 (13)	169, 22 (69)	179, 29 (60)
Southern kingfish	BRD	139, 28 (154)	127, 43 (22)	143, 27 (60)	153, 23 (54)	155, 29 (33)	167, 17 (85)
	Control	139, 25 (311)	138, 34 (40)	141, 29 (99)	155, 26 (210)	157, 26 (103)	173, 16 (120)
Hardhead catfish	BRD	100*, 25 (65)	103, 44 (12)	100*, 38 (86)	94 (1)	301, 52 (2)	150, 50 (2)
	Control	95, 27 (193)	100, 38 (98)	103, 50 (167)	242, 72 (41)	227, 74 (22)	234, 54 (21)
Silver perch	BRD	91, 10 (25)	82*, 14 (116)	87, 12 (106)	104,* 12 (9)	98, 08 (12)	113, 10 (73)
	Control	93, 11 (78)	87, 14 (189)	82, 14 (121)	112, 09 (42)	103, 23 (27)	111, 10 (126)
Pinfish	BRD	84 (1)	— —	130, 35 (4)	79, 05 (49)	76*, 06 (81)	82, 09 (16)
	Control	— —	— —	— —	79, 06 (108)	79, 07 (102)	81, 08 (38)

varied greatly in other studies. This variation has been attributed to temporal and spatial diversity in size and species composition of the finfish and shrimp within a trawling area; changes in bottom substrate; water depth; BRD type, placement, and size; trawl dynamics; and speed, and duration of tow (Branstetter, 1997; Fuls and McEachron[16]).

Although most of the nets tested in these other studies were considerably larger than the nets tested in our study, some of these attributes probably contributed to the variation that we observed. In addition, and most notably, the efficiency of our BRDs was greatly reduced when large numbers of horseshoe crabs were captured or when large numbers of spiny fishes became entangled in the nets.

Although the number and weight of finfish captured were greatly reduced in the FFE-equipped nets, finfish bycatch reduction rates were even higher with the nets equipped with the EMF, particularly the 17-m net, which had the highest overall reduction rate of all BRD and net-

[16] Fuls, B. E., and L. W. McEachron. 1998. Evaluation of bycatch reduction devices in Aransas Bay during the 1997 spring and fall commercial bay-shrimp season. Corpus Christi Bay National Estuary Program Publication CCBNEP-33, 6300 Ocean Drive, Corpus Christi, TX 78412, 33 p.

size combinations. Similar, comparatively high reduction rates for nets equipped with an EMF have been reported elsewhere (Fuls and McEachron[16]).

Both BRDs reduced (usually notably and significantly) the biomass of finfish in all net sizes during both seasons. However, the number of fish in the BRD-equipped nets compared with the control nets varied markedly between seasons. In fall, the number of fish in the BRD-equipped nets was nearly always much lower than the number in the corresponding control nets; but in winter, the number in the BRD-equipped nets was generally slightly higher than the number in the corresponding control nets. This increase was due to the sizable influx of juvenile leopard searobins in the finfish catch in winter. The long pectoral-fin rays on these fish became entangled in the nets (and in the BRD) and prevented the fish from escaping.

The detailed analysis of species-specific change in numbers of fish in the BRD-equipped nets compared with their corresponding control nets revealed additional interesting patterns. The number of silver jennys was reduced in all BRD-equipped nets, except in the 17-m BRD-equipped net during winter. The numbers of hardhead catfish, sand seatrout, silver perch, and southern kingfish were always reduced in the BRD-equipped nets except in the 20-m FFE-equipped net during fall. The number of leopard searobins and blackcheek tonguefish nearly always increased in the BRD-equipped nets, regardless of season. With some exceptions, larger fish were more likely to escape than smaller fish, probably because swimming ability is positively associated with size in fishes (Wardle, 1993). However, fish (particularly large individuals) of species with protruding bony scutes or long fin rays (e.g. gafftopsail catfish, leopard searobin, southern kingfish) became entangled in the nets and thus could not escape. The potential for large individuals of these types of fish to become entangled in the net may have increased because of the restricted net circumference, caused by the presence of the EMF. Thus, for these types of species, mean size of individuals retained in the BRD-equipped nets was frequently larger than mean size of individuals retained in the corresponding control nets.

A number of factors other than morphological features, such as pointed, projecting body structures, influence the ability of fish to escape from trawl nets equipped with BRDs. The behavior of fish in response to trawls has been described as a combination of optomotor response and rheotactic reaction, both of which contribute to a fishes' ability to escape capture in a trawl (Watson[17]). When ambient light conditions and water clarity allow for sufficient contrast between the trawl and the background, many, but not all, fishes orient their heads toward the mouth of trawl and maintain swimming speeds comparable to the trawling speed. Thereby, a fish can align itself with the in-trawl current. This optomotor response is usually associated with the well-developed lateral line system found in pelagic schooling species and is usually absent in demersal species (Pavlov, 1969). However, this response is considerably diminished during nighttime and in turbid water, and both of these conditions existed during our trawling. Thus, fishes with well-developed optomotor responses probably required additional stimuli to escape from our nets, even if they were in close proximity to an escape opening. Most of these fishes may have escaped the trawl through the BRD when the trawl speed was reduced during trawl haul-back (Watson[17]). The rheotactic response allows demersal fish to detect turbulent water flows and associated pressure gradients through the lateral line even when substantial visual cues are not available (Wardle, 1993). Areas of disturbed water exist within a moving trawl, especially near objects such as BRDs, which interrupt water flow. Demersal fishes with well-developed rheotactic responses can sense these areas of reduced velocity, align themselves behind these areas, and eventually escape through the exit provided by the BRD while the trawl is being towed. The finfish species with the largest percentage reductions in numbers in our BRD-equipped nets compared with the corresponding control nets were demersal and most likely used this response to assist in their escape.

[17] Watson, J. W. 1988. Fish behavior and trawl design: potential for selective trawl development. *In* Proceedings of the world symposium on fishing gear and fishing vessel design, (S. G. Fox and J. Huntington, eds.), p. 25–29. Newfoundland and Labrador Institute of Fisheries and Marine Technology, P.O. Box 4920, St. John's, Newfoundland A1C 5R3.

BRDs and fishery management

Both the FFE and EMF are standard bycatch reduction devices recommended by NMFS and used by the shrimp industry. The effectiveness of these two BRDs in reducing finfish bycatch without greatly reducing shrimp catches has been well documented for the Gulf and the South Atlantic shrimp fisheries. (Captiva and Rivers, 1960; Gutherz and Pellegrin, 1988; Murray et al., 1992; Watson et al., 1993; Branstetter, 1997; Rogers et al., 1997; Coleman et al.[7]; Christian et al.[13]; McKenna and Monaghan[14]; Watson et al.[15]; our study). The FFE is now required in all shrimp trawls used in the federal Exclusive Economic Zone along the South Atlantic and in the Gulf.

The policy set forth by the FMFC in 1990 to reduce the overall finfish bycatch in the Florida shrimp fishery has been addressed in our study. In part as a result of this study, Florida is the first state bordering on the Gulf of Mexico to require the use of BRDs in state waters. BRDs not only serve to conserve natural marine resources, in the Florida shrimp fishery they provide additional benefits to the shrimp fishermen. Reducing bycatch decreases drag during tow times, which, in turn, lowers fuel consumption thereby reducing fuel costs, diminishes wear and tear on the trawl gear, decreases culling time by the deck crew, and produces a better shrimp product. From a cost-benefit perspective, BRDs clearly provide conservational, economic, and sociological benefits that far outweigh their actual costs.

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Severe decline in abundance of the red porgy (*Pagrus pagrus*) population off the southeastern United States

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Abstract–Status of the southeastern U.S. stock of red porgy (*Pagrus pagrus*) was estimated from fishery-dependent and fishery-independent data, 1972–97. Annual population numbers and fishing mortality rates at age were estimated from virtual population analysis (VPA) calibrated with fishery-independent data. For the VPA, a primary matrix of catch at age was based on age-length keys from fishery-independent samples; an alternate matrix was based on fishery-dependent keys. Additional estimates of stock status were obtained from a surplus-production model, also calibrated with fishery-independent indices of abundance.

Results describe a dramatic increase in exploitation of this stock and concomitant decline in abundance. Estimated fully recruited fishing mortality rate (F) from the primary catch matrix increased from 0.10/yr in 1975 to 0.88/yr in 1997, and estimated static spawning potential ratio (SPR) declined from about 67% to about 18%. Estimated recruitment to age 1 declined from a peak of 3.0 million fish in 1973–74 to 94,000 fish in 1997, a decline of 96.9%. Estimated spawning-stock biomass declined from a peak of 3530 t in 1979 to 397 t in 1997, a decline of 88.8%. Results from the alternate catch matrix were similar. Retrospective patterns in the VPA suggest that the future estimates of this population decline will be severe, but may be less than present estimates.

Long-term and marked declines in recruitment, spawning stock, and catch per unit of effort (both fishery-derived and fishery-independent) are consistent with severe overexploitation during a period of reduced recruitment. Although F prior to 1995 has generally been estimated at or below the current management criterion for overfishing (F equivalent to SPR=35%), the recent spawning-stock biomass is well below the biomass that could support maximum sustainable yield. Significant reductions in fishing mortality will be needed for rebuilding the southeastern U.S. stock.

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New analyses of the red porgy (*Pagrus pagrus*) stock off the southeastern U.S. coast indicate that dramatic changes in age structure and population abundance have occurred over the last 25 years. The red porgy, a protogynous sparid also known as silver snapper and pink snapper, associates with reefs and is commonly found over irregular and low-profile hard bottoms at depths between about 20 and 200 m (Manooch and Hassler, 1978). The species has been an important component of the snapper-grouper complex in the coastal Atlantic Ocean off the southeastern United States, particularly off North and South Carolina.

This study is the first complete assessment of red porgy in this region since 1986 (Vaughan et al., 1992). We introduce methodological improvements that strengthen analyses considerably, including fishery-independent data to calibrate the virtual population analysis (VPA), as recommended in a recent review of marine stock assessments (NRC, 1998). Extensive analyses were made of the sensitivity of major results (estimates of abundance and fishing mortality rate) to assumptions. Sensitivity analyses (in the broad sense) included separate VPAs on two catch matrices, one based on fishery-independent age-length keys and the second on fishery-derived keys; estimation with different assumptions about natural mortality rate; a retrospective analysis; alternate treatments of zeroes in an abundance index; and the use of a surplus-production model to provide complementary estimates of stock abundance and management benchmarks. Robustness of major conclusions to these factors and relatively close agreement between estimates from catch-at-age models and production models strengthen the finding that the red porgy stock was severely depleted at the close of 1997.

Range, stock structure, and reproductive biology

Red porgy have an extensive range—they are found off the southeastern U.S. Atlantic coast; in the Gulf of Mexico; off the South American Atlantic coast from Brazil to Argentina; off Portugal and Spain; in the Mediterranean Sea; off west Africa south to the Cape Verde Islands; and around the Azores, Madeira, and Canary Islands. The stock unit analyzed in our study includes fish from U.S. Atlantic waters off North Carolina (NC) south of Cape Hatteras; South Carolina (SC); Georgia (GA); and the east coast of Florida (FL). This range expands that previously defined for the stock, which (Vaughan et al., 1992; Huntsman et al.[1]) included fish only from waters off NC and SC. Within the current stock definition, red porgy have been most abundant from NC and SC waters. Tagging studies

[1] Huntsman, G. R., D. S. Vaughan, and J. C. Potts. 1993. Trends in population status of the red porgy *Pagrus pagrus* in the Atlantic Ocean of North Carolina and South Carolina, USA, 1971–1992. South Atlantic Fishery Management Council, 1 Southpark Circle, Charleston, SC 29407. [Available from Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC, 28516.]

have shown neither long-range migrations nor extensive local movements of adult red porgy (Manooch and Hassler, 1978), nor has circumstantial or anecdotal information suggested such movements. Peak spawning occurs from March through April (Manooch, 1976). Red porgy eggs and larvae are pelagic, hatch 28 to 38 h after fertilization, and can survive transport by ocean currents for 30 days or more (Manooch et al., 1981). Thus, the population off the U.S. Atlantic coast could in theory receive eggs or larvae from the Gulf of Mexico stock. However, because of the distances involved and the variability of ocean currents, the likelihood of significant population mixing in this way seems small, and we adopted the stock boundaries described above.

Red porgy attain maximum size slowly and live relatively long (an 18-year-old specimen is the oldest on record), but maturity occurs far younger. Roumillat and Waltz[2] collected red porgy between 1979 and 1987 along the continental shelf between Cape Fear, NC, and Cape Canaveral, FL, using trawl nets, traps, and hook-and-line gear. Life history information was obtained from 7104 red porgy; 5820 otoliths were examined (including 134 from historical or port samples), of which 5491 had discernable rings; estimation of sex composition was based on 6044 red porgy. Mature gonads were found in 18.8% of females at age 1, 85.2% at age 2, 99.7% at age 3, and 100% at older ages.

Red porgy are protogynous hermaphrodites. Thus, females predominate at smaller size intervals, but males occur in all age groups. Age-specific sex ratios reported by Roumillat and Waltz[2] (their Table 6) were used in our analyses: 89% female at age 1, 91% at age 2, 77% at age 3, 67% at age 4, 59% at age 5 , 51% at age 6, 25% at age 7, and 21% at age 8.

Methods

Fishery-dependent data sources and adjustments

In the study area (Cape Hatteras, NC, through the east coast of FL), three fisheries take red porgy: commercial, recreational, and headboat. Hook-and-line has been the most common commercial gear, but occasional significant landings are taken with trawls and traps. Trawling for red porgy has been banned since 1989 (Amendment 12 [SAFMC[3]]) The recreational fishery includes all recreational fishing from shore, from private boats and from charter boats (for-hire vessels that usually accommodate six or fewer anglers as a group). The headboat fishery (larger for-hire vessels that charge per angler) is sampled separately, and for that reason is distinguished here from other recreational fisheries. Recreational and headboat fisheries, like the commercial fishery, use hook-and-line gear almost exclusively. Data sources for all three fisheries are described in our study and summarized in Table 1.

Commercial fishery Landings statistics in weight for the commercial fishery, 1972–97, were obtained from the NMFS general canvass database (NMFS, Southeast Fisheries Science Center, Beaufort, NC, and Miami, FL). In addition, North Carolina commercial landing statistics by gear for red porgy were provided by NC Division of Marine Fisheries (NCDMF). Fishery-based length and weight statistics, 1983–97, were obtained from the NMFS Trip Interview Program (TIP) database. Length frequencies from SC commercial landings, 1976–80, were taken from Vaughan et al. (1992).

Commercial landings statistics, 1972–84, are recorded as "porgies," but include some other species. Following Vaughan et al. (1992), we multiplied such non-North-Carolina landings by 0.9 to approximate landings of red porgy only; North Carolina data were corrected by NCDMF before we received them. Commercial landings were available only in weight and were converted to counts by dividing catch in weight by mean weight per fish for the same gear and year. To compute annual mean weights, fish lengths from the TIP database were converted to weight with estimated weight–length relationships, described below.

Annual length-frequency distributions L were developed for commercial hook-and-line gear for each area (Carolinas vs. Florida), 1983–97. Commercial length frequencies for 1972–82 were taken from Vaughan et al. (1992). Because trap and trawl landings have been quite small since the mid–1980s and few fish have been sampled (1611 [trap]; 1455 [trawl], mostly between 1986 and 1988), two overall length-frequency distributions for each gear were used, one for 1972–89 and the other for 1990–97. Gear-specific commercial length-frequency distributions were weighted by catch in number by state to obtain catch at length by gear and state.

Recreational fishery Recreational catch and effort estimates and data on length and weight composition, 1979–97, were obtained from the NMFS Marine Recreational Fisheries Statistics Survey (MRFSS) database (Gray et al., 1994; Marine Recreational Fisheries Statistics, 1999). Fishing modes used by MRFSS include shore-based, private-boat-based, and charter-boat based fishing. Within each mode, three catch types are defined: "A" catches were available to sampling personnel for identification and measurement; "B1" catches were unavailable because they had been used for bait, filleted, discarded dead, etc.; and "B2" catches were unavailable because they had been released. Postrelease mortality of B2 catches was assumed to be 18% (Dixon and Huntsman[4]). Following

[2] Roumillat, W. A., and C. W. Waltz. 1993. Biology of the red porgy *Pagrus pagrus* from the southeastern United States. Data report 1993 MARMAP, South Carolina Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29422-2559.

[3] SAFMC (South Atlantic Fishery Management Council. 2000. Final, amendment number 12 to the fishery management plan for the snapper grouper fishery of the South Atlantic region. South Atlantic Fishery Management Council, Charleston, SC, 159 p. + appendices.

[4] Dixon, R. L. and G. R. Huntsman. 1993. Survival rates of released undersized fishes (abstract). Sixth Annual MARFIN Conference, Atlanta, GA, 12–13 October 1993. [Available from Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC, 28516.]

Table 1

Data sources for analysis of red porgy off the southeastern United States. Sample size n is number of fish lengths measured. Aging data sources are given in Table 2. Symbol N is number of fish, W, weight of fish caught.

Data source	Years	Database	Type	n
Commercial fishery	1972–97	NMFS, general canvass	Landings (W)	—
	1972–97	NC Div. Mar. Fish.	NC landings (W)	—
	1983–97	NMFS trip interview	Lengths and weights	62,042
	1976–80	SCDNR (Vaughan et al., 1992)	Lengths	8855
Recreational fishery (private and charter boats)	1979–97	NMFS MRFSS	Catch (N and W)	—
			Lengths and weights	945
Headboat fishery	1972–97	NMFS headboat survey (NC, SC)	Catch (N and W)	—
			Lengths and weights	44,131
	1976–97	NMFS headboat survey (GA-N.E. FL)	Catch (N and W)	—
			Lengths and weights	1454
	1981–97	NMFS headboat survey (S.E. FL)	Catch (N and W)	—
			Lengths and weights	1166
Fishery-independent	1979–97	MARMAP hook and line	CPE (N) and lengths	2085
	1980–97	MARMAP traps (FL snapper and chevron)	CPE (N) and lengths	10,784

Vaughan et al. (1992), we adjusted the data to avoid duplication from inclusion of headboat landings in charter-boat landings reported by MRFSS, 1979–85.

Mean recreational landings by mode were calculated for 1979–97 and used for 1972–78, a period of minimal exploitation before MRFSS data were collected. Because recreational landings are a small fraction of the total, this procedure, while approximate, was better than assuming landings of zero in that period.

Recreational length-frequency distributions from MRFSS, 1979–97, were weighted by catch (A+B1) in number by mode, wave (2-month interval), and state. The minimal catch associated with shore-based fishing was pooled with the private-boat mode. Headboat length-frequency distributions from MRFSS (1979–85) were not used in development of catch matrices for the recreational fishery because more complete data were available from the headboat sampling program.

Headboat fishery Estimates of headboat catch in numbers and weight and fishing effort in angler-days (Table 1) were obtained from the NMFS (Beaufort, NC) headboat sampling program (Huntsman, 1976; Huntsman et al., 1978). Zero-intercept linear regression analyses on NC and SC data were used to estimate landings from GA to northeast FL and landings from southeast FL, and fishing effort back to 1972. Catch per effort (CPE) in numbers was calculated by dividing annual catch in numbers by annual effort.

Length samples from headboats were not available from GA or FL before 1976, nor from southeast FL before 1981. We used mean length-frequency distributions for 1976–80 to fill in for GA and FL, 1972–75, and length-frequency distributions from GA to northeast FL to fill in for southeast FL, 1976–80. Annual headboat length-frequency distributions from the headboat sampling program, 1972–97, were weighted by catch in numbers caught during that season (January–May, June–August, September–December), and geographic area (NC, SC, GA to northeast FL, southeast FL) to obtain catch in length by season and area.

Development of catch-at-age matrices

Estimates of catch at age in numbers were made by using an approach similar to that of Vaughan et al. (1992). Total catch in numbers (n, scalar) for each combination of time, gear, and area was multiplied by an age-length key (A, matrix of dimension $a \times b$); the product was multiplied by the corresponding length-frequency distribution (L, vector of length b) to obtain catch in numbers at age (N, vector of length a):

$$\mathbf{N} = n \cdot \mathbf{A} \cdot \mathbf{L}. \quad (1)$$

Here, a is the number of ages (for this study, ages 0 to 8^+) and b is the number of length intervals (for this study, 15 intervals of 25 mm each from 200 mm to 550^+ mm).

Age-length keys Separate age-length keys were developed from fishery-dependent and fishery-independent data. Fishery-dependent keys for 1972–74 were those of Manooch and Huntsman (1977); for 1986, those of Vaughan et al. (1992); for 1996–97, those of Potts and Manooch (2002). Keys for 1975–85 and 1987–95 were approximated by linear interpolation from available keys (method of Vaughan et al., 1992).

We constructed fishery-independent keys from samples taken in 1979–94 (Harris and McGovern, 1997) by the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program, a fishery-independent sampling program of the SC Department of Natural Resources. In that study, 8660 red porgy were collected, primarily with hook and line and various traps, and preserved sagittae were used for age estimation. As a compromise between estimating annual keys based on smaller sample sizes and an overall key, which would disguise growth variability over time, we grouped MARMAP aging data into 3-yr periods, with the last four years divided instead into two 2-yr periods: 1979–81, 1982–84, 1985–87, 1988–90, 1991–92, 1993–94. Potts and Manooch (2002) aged 111 red porgy collected during 1996–97 by the MARMAP program (predominantly younger fish, maximum age of 6). We used an age-length key from those data for 1995–97. Where fewer than 10 fish occurred in a 25-mm total-length interval, we pooled the data over longer time periods.

No aging data are available from fishery-independent sources before 1979. We constructed a key, used for 1972–74, from fishery samples taken in those years (Manooch and Huntsman, 1977). For 1975–78, we interpolated linearly between that key and the earliest key derived from fishery-independent data (1979–81). Thus, the fishery-independent (primary) catch matrix described below reflects some fishery-dependent data in the earliest years.

Catch-at-age matrices Equation 1 was applied to each fishery-gear combination and catch-at-age estimates were accumulated for each year to obtain estimates of annual catch in numbers at age (the catch matrix), 1972–97. This was done twice, first by using the fishery-independent age-length keys to obtain the primary catch matrix, and then by using fishery-derived age-length keys to obtain the alternate catch matrix. (Although the designation of "primary" and "alternate" matrices is somewhat subjective, it was based on the more extensive and continuous quality of fishery-independent data, as discussed later. Despite the designation, most analyses were conducted twice, once with each matrix.) Final catch matrices each contained numbers of fish caught at ages 1 through 8+ in fishing years 1972 through 1997; partial recruitment for age-0 red porgy was essentially zero.

We judged coherence of catch matrices by examining pairwise correlations between ages as a cohort progressed through the fishery. For fully recruited ages and with F varying only moderately from year to year, we expected to be able to follow a strong or weak cohort through the catch matrices. Both matrices generally showed significant correlations ($P<0.1$) between lagged catches at adjacent ages. A few significant correlations were found among lagged catches for nonadjacent ages.

Growth in length and weight

Von Bertalanffy (1938) growth models were fitted from data on total length (mm) and age obtained from fishery-independent and fishery-dependent sources (Table 2). Disaggregated aging data could not be located for fishery-dependent data from 1972 to 1974 and from 1986; therefore observed midinterval lengths at age from keys were used for those years. For fishery-dependent data for 1989–98 and fishery-independent data for 1996–97, back-calculated length at oldest age was used, a procedure that avoids potential bias by the use of multiple measurements per fish (Vaughan and Burton, 1994). For fishery-independent data, 1979–94, observed length at age was used, adjusted for month of collection. The particularly high standard error associated with the estimate of L_∞ for fishery-independent data, 1996–97, was associated with a lack of fish older than 6 years of age in the sample (Table 2).

We estimated weight W (in kg) from total length L (in mm) by using the relationship $W = aL^b$. Parameter estimates were as follows: for fishery-dependent modeling, we used values from Manooch and Huntsman (1977) ($a = 2.524 \times 10^{-5}$ and b=2.894) for the 1970s and 1980s; and from Potts and Manooch (2002; a=8.85 × 10^{-6} and b=3.060) for the 1990s. For fishery-independent modeling, we used values for 1972–78 from Manooch and Huntsman (1977), and we estimated values for 1979–97 from MARMAP data, 1979–94, (a=3.064 × 10^{-5} and b=2.865).

Abundance indices

Fishery-independent data on length, weight, age, and CPE, 1979–97 (Table 1) were obtained through the MARMAP program (Collins and Sedberry, 1991; Harris and McGovern, 1997). In computing fishery-independent indices of abundance from those data, we used CPE from hook-and-line and trap gears only. We extended data from chevron trap, 1988–97, back to 1980 with data on Florida snapper trap, using a conversion factor determined by MARMAP (Collins, 1990; Vaughan et al., 1998); we refer to the resulting series as "extended" chevron trap. To obtain age-specific indices of abundance for hook-and-line, 1979–97, and extended chevron trap, 1980–97, we applied Equation 1, using CPE in place of n, and using annual MARMAP estimates of CPE, age-length keys, and length-frequency data for each gear.

Like the catch matrices, matrices of fishery-independent CPE estimates were examined for coherence through correlations among lagged CPE. The hook-and-line index showed greatest coherence among ages 1 through 4, whereas the extended chevron-trap index appeared quite coherent over a wider range of older ages (3 through 7).

Mortality estimation

Instantaneous total mortality rates (Z) were estimated from cohort-specific catch-curve analyses (Ricker, 1975) of the two catch matrices by using only ages that appeared fully recruited (4 through 7). Empirical approaches were also used to estimate total mortality rate (Z). The more complex of two methods presented by Hoenig (1983) is based on age of the oldest fish observed, sample size, and age of recruitment to the sampling procedure. Assuming those quantities to be 18 yr, 10,000 fish, and 1 yr, we estimated Z = 0.58/yr, a likely upper bound on M.

Table 2

Parameters of von Bertalanffy growth models for red porgy off southeastern United States. Maximum age in the sample is labeled t_{max}; sample size is n. Parameters estimated from observed mid-interval length at age in fishery-dependent data for 1972–74 and 1986; from back-calculated length at oldest age in fishery-dependent data for 1989–1998 and fishery-independent data for 1996–97; and from observed length at age adjusted for month of collection in fishery-independent data for 1979–94. Asymptotic standard error is in parentheses below corresponding parameter estimate.

Type of data and year	n	L_∞ (mm)	k	t_0	$t_{max\ (yr)}$	Range (mm)
Fishery-dependent data						
1972–74	1685	575.8	0.16	–1.88	15	185–640
		(2.5)	(0.002)	(0.03)		
1986	535	1252.9	0.40	–4.05	12	213–615
		(28.7)	(0.001)	(0.04)		
1989–98	492	796.6	0.09	–2.34	18	247–723
		(43.9)	(0.009)	(0.23)		
Fishery-independent (MARMAP) data						
1979–94	8601	485.5	0.23	–1.48	14	142–568
		(5.3)	(0.01)	(0.06)		
1979–81	1171	501.3	0.34	–0.15	13	142–557
		(5.4)	(0.01)	(0.06)		
1982–84	2159	626.1	0.15	–1.61	14	145–568
		(24.6)	(0.01)	(0.14)		
1985–87	2332	542.5	0.16	–2.24	12	176–523
		(20.4)	(0.01)	(0.16)		
1988–90	1268	424.2	0.31	–1.06	12	176–487
		(8.6)	(0.02)	(0.14)		
1991–92	842	425.1	0.25	–1.62	13	179–456
		(10.1)	(0.02)	(0.20)		
1993–94	829	375.7	0.43	–0.78	12	183–501
		(5.5)	(0.04)	(0.18)		
1996–97[1]	111	754.7	0.10	–1.27	6	151–384
		(246.3)	(0.05)	(0.38)		

[1] Otoliths from fish collected during 1996–97 by MARMAP but aged by C. Manooch and J. Potts (NOAA Beaufort Laboratory).

We estimated natural mortality rate empirically (Pauly, 1979) from parameters L_∞ and K of the von Bertalanffy growth function and mean environmental temperature. Estimates ranged from M = 0.27/yr to M = 0.57/yr, based on mean sea temperature of 22°C (Manooch et al., 1998) and the range of growth parameters estimated in our study (Table 2). A similar method, that of Ralston (1987) and based solely on growth parameter K, provided estimates from M = 0.22/yr to M = 0.64/yr. Given the uncertainty in M, we chose a base M = 0.28/yr (Vaughan et al., 1992). We also performed bracketing estimates of most quantities using M = 0.20/yr and M = 0.35/yr.

Fishing mortality rate F was estimated by subtracting the assumed natural mortality rate from the total mortality rate. These estimates of F were used only as terminal-year values in the separable VPA.

Virtual population analyses

Primary and alternate catch matrices were analyzed by using virtual population analysis (VPA) to obtain annual age-specific estimates of F and population size. First, a separable VPA (Doubleday, 1976; Pope and Shepherd, 1982), as implemented by Clay (1990), was used to estimate partial recruitment by age for later use in calibrated VPA. Data from 1992–97 were used for this purpose because a 12-inch minimum size limit was introduced in 1992 (amendment 4[SAFMC[5]]), and using data from both before and after imposition of the size regulation would likely violate the separability assumption. The starting value of F for the separable VPA was the mean of three final year-class estimates of Z (~0.78/yr), less M.; i.e. F ~ 0.50/yr.

A calibrated VPA (Pope and Shepherd, 1985; Gavaris, 1988) was then applied, as implemented in the FADAPT

[5] SAFMC (South Atlantic Fishery Management Council). 1991. Final, amendment 4, regulatory impact review, initial regulatory flexibility analysis and environmental assessment for the fishery management plan for the snapper grouper fishery of the South Atlantic region. South Atlantic Fishery Management Council, Charleston, SC, 99 p. + appendices.

computer program,[6] by using the two fishery-independent abundance indices (hook-and-line and extended chevron trap). Most calibrated VPA runs were made with both indices, but a few were made with individual indices to assess sensitivity. The hook-and-line index included estimates of zero in 1992 and 1996, to which a small value (0.0001) was added before log transformation, a technique often used in statistical ANOVA models (e.g. Snedecor and Cochran, 1980). Effects of that approach were explored by assuming missing values in place of zeroes in an additional calibrated VPA run.

Several additional techniques were used to examine sensitivity to assumptions. Sensitivity of estimated F and recruitment to age 1 to uncertainty in M was investigated by conducting the separable and calibrated VPAs with alternate values of M (0.20/yr and 0.35/yr). Retrospective analyses of the calibrated VPA were conducted to investigate the possibility of systematic deviations ("retrospective patterns") in estimates of F and recruitment in most recent years, in comparison to estimates obtained for the same years from later analyses. In the retrospective analyses, we varied the final year of data used from 1992 to 1997; the initial year was 1972 throughout.

For presentation of results, we averaged estimated quantities within three time periods: 1972–78, representing a lightly fished stock; 1982–86, representing the stock after increasing exploitation during the early 1980s; and 1992–96, representing conditions since the last major change in management (amendment 4[SAFMC[5]]), but omitting the terminal year (1997) to reduce retrospective effects (discussed below). We refer to these as early, middle, and recent periods. Recruitment was defined as the number of fish at age 1 on January 1.

Yield per recruit

Equilibrium yield per recruit (YPR) was estimated by the method of Ricker (1975), which divides the exploited life span into phases of constant mortality and growth rates; total YPR is obtained by summing yield across phases. Parameter estimates from YPR analysis were for both sexes and across the three time periods described above. It has long been recognized that fishing at F_{max} (F that maximizes YPR) can cause recruitment failure (Gulland and Boerema, 1973; Clarke, 1991; Caddy and Mahon, 1995), and the reference point $F_{0.1}$ was introduced as a more conservative alternative (Gulland and Boerema, 1973). Using most recent growth and selectivity, we computed both F_{max} and $F_{0.1}$.

Spawning potential ratio

Static spawning potential ratio (static SPR)—also known as equilibrium SPR or maximum spawning potential (Gabriel et al., 1989)—is a measure of fishing mortality rate scaled to a species' biology. Static SPR for a given fishing mortality rate F^* is computed as the ratio SPR = SS(F^*) / SS(0), where SS(F^*) is the spawning-stock size (lifetime cohort spawning contribution) expected under F^*, and SS(0) is the corresponding spawning-stock size expected under $F = 0$. Other life history parameters are assumed constant at most recent values. Increases in F reduce static SPR.

In species that do not change sex, spawning-stock biomass is usually computed as total mature female biomass or total egg production (Prager et al., 1987), quantities that are highly correlated. Because red porgy change sex, we used four representations of spawning-stock biomass: female mature biomass, male mature biomass, total (male + female) mature biomass, and total egg production, each assuming the sex ratios at age given above (Roumillat and Waltz[2]).

To compute total egg production, we used the relationship between fecundity (E, number of eggs) and total length (TL, mm) of Manooch (1976):

$$\ln E = -14.1325 + 4.3598\,(\ln TL), \quad (2)$$

Sex ratio in the mature population can be changed by fishing. We estimated reduction in the proportion of males among mature fish from the proportion expected with no fishing and assuming that the rate of sex transformation is not affected by changes in population structure.

Spawner-recruit relationships

The relationship between spawning-stock biomass and resulting recruitment to age 1 was modeled by using the Beverton-Holt spawner–recruit function (Ricker, 1975):

$$R = \mathrm{SSB}/(b_0 \times \mathrm{SSB} + b_1), \quad (3)$$

where R = recruitment;
SSB = spawning-stock biomass, and
b_0, b_1 = fitted parameters.

To reduce the influence of retrospective patterns, SSB and R series (estimated from VPA) used in recruitment modeling were terminated at 1992. We used total mature biomass, rather than the more usual female mature biomass, to represent SSB in recruitment modeling.

With the estimated stock-recruitment relationship, 500-year simulations of the stock were made to estimate equilibrium yield and spawning-stock biomass as functions of fishing mortality rate. The simulations used mean population numbers, 1992–96, as starting values. Age-specific selectivity for the same period and the most recent growth patterns were used throughout. We thus estimated MSY, B_{MSY}, and F_{MSY} for each catch matrix.

Surplus-production model

A surplus-production model was fitted to obtain additional estimates of management benchmarks and stock status. We used the Prager (1994, 1995) formulation and implementation of the continuous-time Graham-Schaefer (logis-

[6] FADAPT by V. R. Restrepo (International Commission for the Conservation of Atlantic Tunas, Calle Corazón de María, 8, Sixth Floor, 28002 Madrid, Spain).

tic) model (Schaefer, 1954, 1957; Pella, 1967; Schnute, 1977; Prager, 1994). The approach is an observation-error estimator assuming proportional error variance and conditioned on observed landings. We attempted to fit the generalized production model (Pella and Tomlinson, 1969; Fletcher, 1978) by similar methods. Data were total landings in weight, 1972–97, and CPE indices derived separately from fishery-independent hook-and-line and trap data, 1979–97.

Initial difficulty in obtaining estimates was traced to two years of zero CPE in the fishery-independent hook-and-line index. Because the fitting was conducted in logarithmic transform, zeroes could not be accommodated; our initial, unsuccessful approach was to substitute very small values. We obtained estimates through the alternate procedure of considering those values missing, which is statistically equivalent to setting the observation weights to zero.

Because some estimates were moderately sensitive to assumptions about the starting stock biomass, B_1, in relation to carrying capacity, K, we obtained estimates at a range of values, namely B_1/K = {0.55, 0.65, 0.75, 0.85, 0.95} , a range chosen to reflect the stock's lightly fished status before the first year (1972). Fixing the starting value of relative biomass can reduce variance of estimates considerably (Punt, 1990). Bootstrapping with 700 repetitions was used to estimate 80% bias-corrected confidence intervals (Efron and Tibshirani, 1986) on the central set of estimates (B_1/K=0.75).

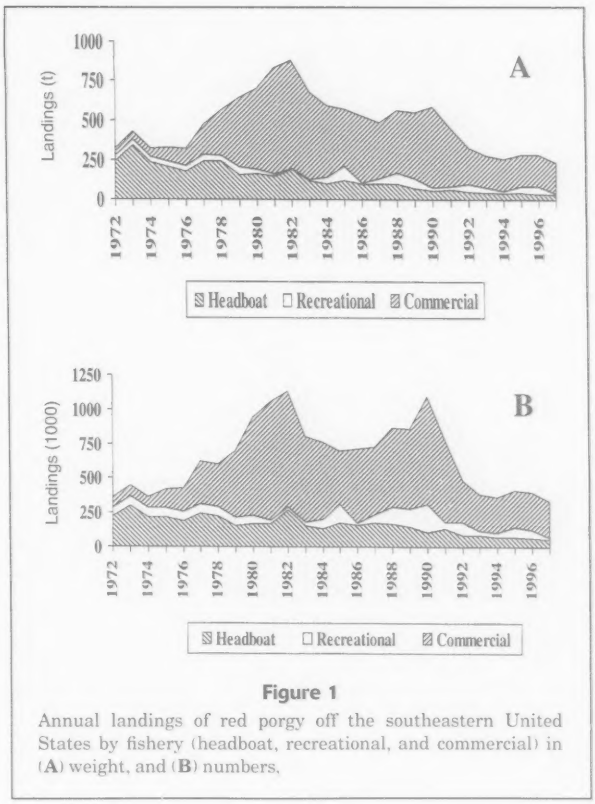

Figure 1

Annual landings of red porgy off the southeastern United States by fishery (headboat, recreational, and commercial) in (**A**) weight, and (**B**) numbers.

Results

In this section, all results are reported for the base value of M = 0.28/yr unless otherwise stated. Results reflect analysis of the primary catch matrix unless use of the alternate matrix is specifically mentioned.

Summary of landings and CPE

During the study period (1972–97), total landings in weight rose from about 325 t in 1972 to a maximum of 880 t in 1982 (Fig. 1A). Landings have been at or below 300 t since 1992, with 234 t in 1997. The headboat fishery accounted for about 52%–80% of total landings through 1977; commercial landings have been most prevalent since (Fig. 1B, Table 3). Maximum landings in numbers were about 1.13 million fish in 1982 (Table 4).

Commercial landings in weight rose from 45 t in 1972 to 678 t in 1982 and declined to 200 t/yr or less since 1992 (Fig. 1A); landings in numbers had a similar pattern (Fig. 1B). Commercial trawl landings averaged about 14% of commercial landings, 1972–84 but were quite small by 1985, and trawl gear was prohibited as of 12 January 1989 by amendment 1 to the Fishery Management Plan (amendment 12 [SAFMC[3]]). Hook-and-line landings have been about 95% of commercial landings by weight since 1985.

Recreational landings in numbers have shown no consistent trend, averaging about 70,000 fish per year, with some outstanding years of more than 100,000 fish between 1985 and 1990 (Fig. 1B). Catch by mode of fishing has been highly variable, but recreational landings have mainly been taken by charter boat (43% by number during the 1990s) and private boat (55%). Although remaining landings (<3%) are attributed to fishing for red porgy from shore, this amount is unlikely to be correct. These records may result from errors in recorded fishing mode or from erroneous species identification, but in either case would have negligible effect on our analyses.

Headboat landings have declined from 200,000 fish/yr during the 1970s to around 100,000–200,000 fish/yr in the 1980s and fewer than 100,000 fish/yr since (Fig. 1B). Most landings have come from NC and SC.

Mean weight in the commercial hook-and-line and headboat fisheries in the Carolinas has decreased, especially since about 1978 (Fig. 2). Mean weight in all fisheries combined has shown a general decline from 1972 to 1991 (Fig. 2) but has since increased somewhat.

All data on catch per effort (CPE) exhibited long-term decline. Declining headboat CPE was apparent from both NC and SC (Fig. 3). The fishery-independent abundance indices, also based on CPE, showed corresponding declines (Fig. 3): the extended chevron-trap index decline was precipitous; that in the hook-and-line index was similar, but somewhat less dramatic. (The CPE series derived from

Table 3

Red porgy landings in numbers (1000) by fishery, area, and gear or mode. Listed recreational landings from private boats include minor landings from shore.

	Commercial						Recreational and headboat							
	NC + SC			GA + FL			NC + SC			GA + FL				
Year	Trawl	Traps	Lines	Trawl	Traps	Lines	Private	Charter	Headboat	Private	Charter	Headboat	Commercial	Recreational and headboat
1972	0.6	22.9	0.9	0.2	1.3	45.4	31.7	27.1	201.4	9.9	1.0	18.6	71.1	289.7
1973	13.5	9.8	2.1	0.0	0.2	50.9	31.7	27.1	274.4	9.9	1.0	25.3	76.4	369.4
1974	0.0	20.3	3.5	0.0	0.5	47.5	31.7	27.1	201.3	9.9	1.0	18.6	71.8	289.5
1975	1.2	31.5	3.0	0.0	0.5	95.7	31.7	27.1	197.3	9.9	1.0	18.2	131.9	285.2
1976	9.0	28.9	24.4	36.2	0.4	67.9	31.7	27.1	173.8	9.9	1.0	12.9	166.7	256.4
1977	55.2	12.9	33.3	112.9	3.2	92.3	31.7	27.1	218.9	9.9	1.0	24.7	309.8	313.3
1978	6.9	0.2	136.2	1.0	0.0	163.6	31.7	27.1	176.4	9.9	1.0	47.4	307.9	293.4
1979	87.0	3.3	253.0	0.0	0.0	140.8	37.5	2.0	128.8	14.8	3.0	27.8	484.0	213.9
1980	271.3	7.9	211.7	52.4	0.0	166.4	8.7	7.8	148.7	40.5	4.2	19.8	709.7	229.7
1981	276.4	16.4	342.2	50.9	0.0	174.0	8.1	15.1	156.9	3.9	0.1	11.1	859.9	195.2
1982	212.3	8.6	450.1	30.1	0.0	139.5	5.1	10.0	265.0	6.3	0.0	7.9	840.6	294.2
1983	114.0	17.4	378.1	6.9	0.0	104.5	18.3	9.7	152.7	0.9	0.1	3.1	621.0	184.7
1984	60.7	17.6	301.5	17.6	0.2	158.5	5.7	67.4	124.4	0.0	1.0	5.6	556.0	204.1
1985	0.0	2.6	231.5	6.8	0.2	142.4	45.4	1.9	167.1	89.9	0.8	9.4	383.5	314.5
1986	8.2	25.8	285.8	6.6	0.0	208.1	13.4	2.6	140.8	0.1	0.0	20.3	534.6	177.1
1987	6.9	19.1	308.3	0.0	0.0	156.5	44.2	16.1	151.0	1.9	0.0	22.6	490.9	235.7
1988	28.2	19.3	369.3	0.2	4.0	146.6	57.8	66.9	157.9	3.3	0.0	10.6	567.5	296.5
1989	0.0	21.1	389.2	0.0	4.9	164.6	37.4	95.1	137.4	0.0	0.0	9.1	579.8	279.0
1990	0.0	80.5	436.8	0.0	16.5	248.4	197.7	13.8	97.5	0.9	0.0	7.3	782.2	317.1
1991	0.0	93.7	324.3	3.3	5.5	173.7	25.6	12.9	122.7	14.5	0.0	7.1	600.6	182.8
1992	0.0	4.4	211.0	2.0	0.2	82.6	29.3	61.3	81.1	3.0	0.0	4.8	300.2	179.6
1993	0.0	14.9	175.0	2.9	8.7	65.6	10.8	18.6	78.5	1.4	4.8	3.2	267.1	117.4
1994	0.0	11.1	189.3	2.2	0.3	53.9	14.7	17.8	67.7	2.5	0.0	2.7	256.8	105.4
1995	0.0	8.4	177.1	4.5	1.4	72.0	3.4	70.0	66.8	1.8	0.4	4.0	263.4	146.2
1996	0.0	6.4	188.4	0.3	0.0	79.8	36.3	17.5	61.2	0.3	5.0	3.7	274.8	124.0
1997	0.0	4.1	172.9	1.1	0.0	90.8	3.6	7.8	49.8	1.3	0.0	4.1	268.8	66.5

Table 4

Primary and alternate catch-in-numbers-at-age matrix for red porgy off the southeastern United States. Matrix is in thousands of fish, is based on fishery-independent age-length keys, and includes 18% (by number) of released recreationally caught fish. Each year's modal age is underlined.

	Age (yr)								
Year	1	2	3	4	5	6	7	8+	Total (1000)
Primary catch-in-numbers-at-age matrix									
1972	13.2	60.7	56.2	55.9	87.3	44.1	23.5	19.0	359.9
1973	13.7	63.0	62.8	64.6	102.4	55.3	36.8	46.3	444.9
1974	13.7	64.8	63.1	58.8	76.9	35.5	21.7	26.0	360.5
1975	16.7	116.5	96.3	51.3	37.4	38.9	28.2	30.3	415.6
1976	13.8	88.3	87.5	60.4	56.4	46.1	32.5	36.7	421.7
1977	12.9	92.7	102.4	88.9	106.0	78.2	60.2	80.5	621.9
1978	15.3	101.0	106.2	88.2	115.6	69.1	46.9	58.0	600.3
1979	13.9	134.4	145.5	90.6	57.9	95.5	78.4	81.0	697.2
1980	14.6	153.9	212.2	128.6	76.6	121.6	100.2	130.9	938.6
1981	16.3	206.5	218.3	215.6	156.6	86.8	55.7	99.2	1055.1
1982	24.7	289.8	246.1	218.6	147.7	76.5	47.3	83.9	1134.8
1983	35.6	128.2	184.0	185.5	98.2	65.6	45.5	63.0	805.7
1984	31.1	137.7	202.5	186.6	85.5	50.8	28.3	37.5	760.0
1985	34.1	116.4	118.1	155.6	127.6	84.3	38.0	24.0	698.0
1986	29.0	143.4	134.9	160.6	118.6	71.3	32.5	22.3	712.7
1987	71.8	227.2	176.9	95.9	38.3	44.4	32.4	39.0	725.8
1988	87.9	288.7	219.0	109.0	42.2	46.8	30.5	38.2	862.4
1989	40.0	232.9	247.2	122.9	92.5	37.5	36.6	46.8	856.3
1990	66.2	325.1	322.5	146.1	105.2	40.2	40.3	49.9	1095.4
1991	46.7	160.4	162.9	181.1	97.5	54.9	29.6	49.9	783.0
1992	19.6	63.7	95.7	124.2	73.3	42.1	22.0	38.9	479.4
1993	3.9	38.9	53.2	95.7	94.7	51.0	24.0	23.2	384.5
1994	3.3	32.5	47.7	89.2	91.0	50.4	24.7	23.5	362.2
1995	5.2	39.9	54.7	98.0	97.2	52.6	23.8	24.1	395.5
1996	4.9	44.9	57.9	99.9	95.6	50.6	21.5	21.1	396.3
1997	2.3	31.9	46.2	85.3	85.2	45.2	20.2	18.8	335.2

continued

headboat catches are shown for comparison, but were not used in calibrating VPAs.)

In the primary catch matrix, modal age (underlined in Table 4) varied between 2 and 5; age 4 has been most common in recent years. Modal age in the alternate catch matrix (Table 4) was similar, but showed less annual variation, probably because of interpolation across years of the age-length keys. A few strong year classes have moved through the population, most notably those that were age 2 in 1987–90, but no strong year classes have followed. The modal age has increased since 1992, the year in which a 12-inch minimum size limit was imposed (amendment 4 [SAFMC[5]]).

Trends in mortality and recruitment

In our calibrated VPAs, ages 4 through 7 were always considered fully recruited, and estimates of F were typically averaged over those ages, weighted by population numbers at age. Those weighted averages are referred to here as full F.

In analysis of the primary catch matrix, estimates of F for all ages were lowest in the early years (Table 5). Fishing mortality on ages 1–3 increased between the early and middle periods and then declined, but full F (ages 4+) increased and remained high. This pattern probably reflects the imposition of the 12-inch TL minimum size limit in 1992 with amendment 4 (SAFMC[5]). Estimates of F from the alternate catch matrix in the recent period were generally higher for ages 3+ than estimates from the primary catch matrix. Slightly lower estimates of F in the recent time period were obtained from the primary catch matrix when missing values, rather than small numbers, replaced zeroes in computing the hook-and-line index.

Estimates of full F from both catch matrices started low, rose abruptly from the late 1970s to 1982, decreased some-

Table 4 (continued)

Year	Age (yr) 1	2	3	4	5	6	7	8+	Total (1000)
Alternate catch-in-numbers-at-age matrix									
1972	13.2	60.7	56.2	55.9	87.3	44.1	23.5	19.0	359.9
1973	13.7	63.0	62.8	64.6	102.4	55.3	36.8	46.3	444.9
1974	13.7	64.8	63.1	58.8	76.9	35.5	21.7	26.0	360.5
1975	18.7	71.0	79.4	78.7	74.7	40.6	21.5	31.7	416.2
1976	15.2	57.6	69.1	79.7	85.8	49.2	26.6	39.0	422.2
1977	14.2	65.6	83.3	105.3	128.4	82.8	52.8	89.9	622.3
1978	16.6	78.5	99.0	102.4	121.2	75.2	43.9	63.7	600.5
1979	15.2	78.2	98.4	116.6	150.7	99.9	59.3	79.7	697.9
1980	15.8	86.0	129.2	171.7	213.4	116.6	70.1	136.6	939.3
1981	12.6	93.9	149.2	197.9	247.8	136.6	86.2	131.2	1055.1
1982	18.7	150.5	191.4	216.7	252.0	122.2	73.9	109.5	1134.8
1983	41.5	132.9	135.4	146.2	162.0	70.3	48.7	69.0	805.8
1984	36.4	145.9	154.0	151.0	153.5	54.5	27.9	36.8	760.1
1985	27.5	120.7	142.0	140.3	156.6	56.3	25.8	28.9	698.0
1986	25.2	120.5	159.5	169.0	131.4	52.3	23.0	31.7	712.7
1987	6.9	88.3	204.0	180.5	129.8	56.4	26.1	34.6	726.6
1988	15.4	111.7	262.3	224.5	141.3	53.8	23.8	31.3	864.0
1989	15.1	132.5	255.2	199.0	140.6	58.5	25.2	32.7	858.8
1990	32.5	216.4	330.7	247.5	158.7	57.7	23.0	32.9	1099.4
1991	22.5	165.6	238.3	180.9	104.5	34.4	14.7	22.6	783.4
1992	10.5	65.6	138.4	129.1	86.9	28.8	9.6	11.0	479.8
1993	1.9	29.8	104.6	125.7	80.5	24.6	8.4	9.1	384.5
1994	1.8	27.2	91.9	119.7	79.7	24.1	9.0	9.0	362.3
1995	3.6	37.7	108.4	128.4	81.1	21.6	6.8	7.9	395.5
1996	0.3	9.1	104.6	142.5	89.8	30.4	9.2	10.6	396.3
1997	0.1	3.3	76.9	125.8	83.9	28.4	8.1	8.8	335.2

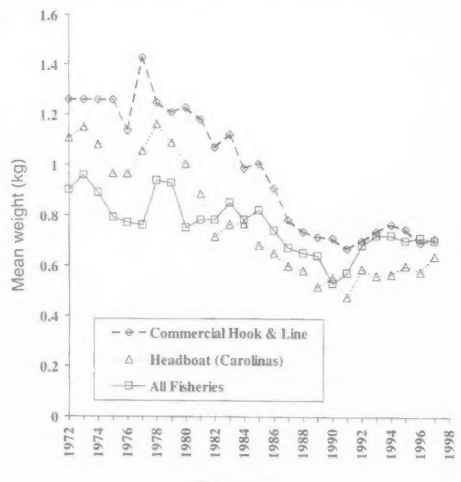

Figure 2

Annual mean weight of red porgy off the southeastern United States in landings from commercial hook-and-line, headboats from the Carolinas, and from all fisheries. Minimum size limit was introduced in 1992.

what, and gradually increased through the present (Fig. 4A). Of the two matrices, the primary matrix provided lower estimates of full F in the recent period, particularly with zeroes replaced by missing values.

Estimates of recruitment were not particularly sensitive to estimation procedure. A general decline in recruitment, 1973–97, was estimated from both catch matrices and with either treatment of zeroes (Fig. 4B).

Sensitivity runs on the primary catch matrix, but with M = 0.20/yr or M = 0.35/yr, estimated that patterns in F and recruitment were similar to those with the base value of M = 0.28/yr (Fig. 5). Under the assumption M = 0.20/yr, estimated values of F were higher than the base assessment; whereas under the assumption M = 0.35/yr, estimated values of F were lower (Fig. 5A). Effect of the value of M on recruitment increased with each year backwards in time. Regardless of the value of M, the pattern of estimates was of initially high recruitment, followed by a long period of severe decline (Fig. 5B).

For comparative purposes, VPA fits were also made by using only the hook-and-line index or only the extended chevron-trap index. Essentially no differences were noted in estimates of full F or recruitment to age 1.

In our VPAs, we estimated statistical weights for the two calibration indices. Estimated weights varied only slightly

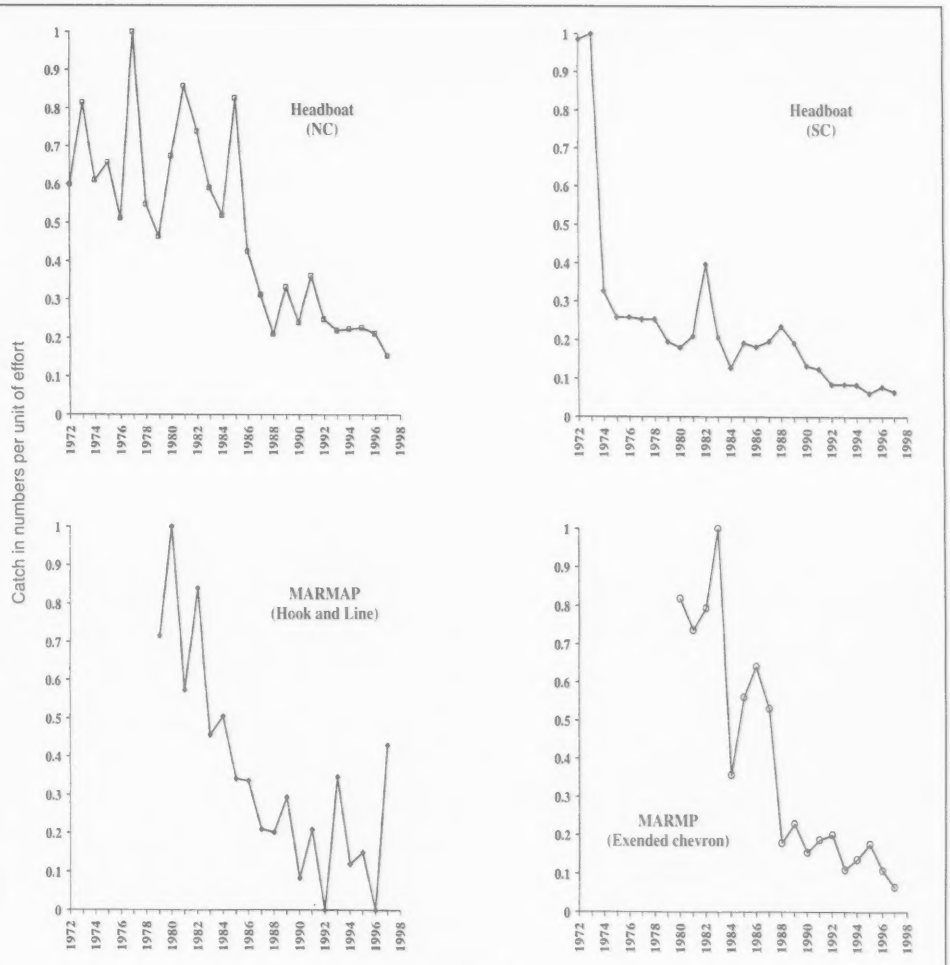

Figure 3

Catch per effort (standardized to series maximum) from the headboat fishery in North and South Carolina (fish caught per angler day, 1972–97); and from MARMAP sampling by gear (hook-and-line, 1979–97; and extended chevron trap, 1980–97), for red porgy off the southeastern United States.

with different assumptions about M. Base analysis of the primary catch matrix estimated weights of 0.08 for hook-and-line CPE and 0.92 for extended chevron-trap CPE; analysis of the alternate catch matrix estimated weights of 0.05 and 0.95. When missing values were used in place of zeroes in the hook-and-line index, estimated weights were 0.50 for hook-and-line CPE and 0.50 for extended chevron trap CPE, demonstrating that treatment of zeroes is an important consideration. The main change in results from using missing values was decreased estimates of F in recent years (Fig. 4A).

In the retrospective analysis, estimates of F generally converged in about 3 to 4 years; convergence in estimates of recruitment took a year or two longer (Fig. 6). A large positive retrospective pattern was evident in full F in the most recent year, and a corresponding negative pattern in estimates of recruitment (Fig. 6). The retrospective pattern was similar when using missing values for zeroes.

Yield per recruit and related benchmarks

Estimates of equilibrium YPR were somewhat sensitive to the value of M assumed, with larger assumed values of M corresponding to smaller estimates of YPR. The highest YPR was obtained during the middle time period (Table 6); however, high theoretical values of yield per recruit can result from fishing mortality rates that are not sustainable.

The two biological reference points F_{max} and $F_{0.1}$ (Beverton and Holt, 1957; Sissenwine and Shepherd, 1987) were estimated from the yield-per-recruit analysis. Assuming

partial recruitment based on average F at age, these reference points were estimated for the recent time period from the primary and alternate catch matrices as F_{max} = 0.5/yr and 0.7/yr, respectively; and $F_{0.1}$ = 0.23/yr and 0.25/yr, respectively (Table 7).

Spawning potential ratio, spawning-stock biomass, and stock-recruitment model

Estimates of static SPR were calculated by catch matrix, time period, and assumed value of M and for four measures of spawning biomass (total mature biomass, mature female biomass, mature male biomass, and egg production) (Table 6; Fig. 7). Static SPR based on mature female biomass was less affected by increases in F than static SPR based on mature male biomass because younger fish are predominantly female and older fish, male. For example, full F that produced 59% SPR in mature female biomass produced 49% SPR in egg production, 42% SPR in total mature biomass, and 27% SPR in mature male biomass (Table 6).

Corresponding estimates were made of reduction in the proportion of males due to fishing in the three periods. For example, a value of 69% in the last column of Table 6 means that if the proportion of males in the mature unfished population had been 50%, introduction of fishing mortality would reduce this proportion to 34.5% of the population (69% × 50%). These estimates were made on the basis of observed sex ratios at size and assuming that the rate of transformation from female to male does not increase as the population is fished down.

Total spawning stock biomass (SSB) was estimated from the primary catch matrix to have reached its peak in about 1979 at 3530 t, declining to 397 t in 1997 (Fig. 8A). When missing values were substituted for zeroes in computing the CPE index, estimates of SSB near the end of the series were slightly higher (Fig. 8A). Estimates from the alternate matrix were similar, with the largest differences occurring before 1983 (Fig. 8A).

Static SPR estimated from the primary catch matrix was high during the 1970s, reached 67% in 1975, and declined to a minimum of 33% in 1982, increased again to 55% in 1993, and declined to about 18% in 1997 (Fig. 8B). Estimates from the alternate catch matrix were similar, but markedly lower from 1983 to 1994 (Fig. 8B). Values of full F providing spe cified values of static SPR (based on female egg production and total spawning stock biomass) are summarized in Table 7, along with values of full F averaged by period, for comparative purposes.

The recent management definition of overfishing is static SPR <35% (amendment 12 [SAFMC[3]]). Our primary estimates are of static SPR >35% from 1972 to 1994 (except for 1982), lower thereafter. Estimates from the alternate catch matrix show static SPR >35% from 1972 to 1980, lower thereafter.

During the early to mid 1970s, a large spawning stock produced high recruitment. Despite a high spawning-stock size estimated through about 1983, SPR and recruitment declined, and the unsustainable landings of the late 1970s and 1980s reduced the spawning stock to levels not expected (under the stock–recruitment model) to provide good recruitment. Similar patterns were apparent in stock-recruitment curves derived from both catch matrices (Fig. 9).

Table 5

Mean estimates (from calibrated virtual population analyses) of age-specific instantaneous fishing mortality rate (F) on red porgy off southeastern U. S. during three time periods. Estimates from primary catch matrix (see text) are given for three levels of natural mortality rate M, two treatments of missing values for M=0.28. Estimates from alternate catch matrix given for M = 0.28 only. Exploitation rate in final column is based on catch of ages 1–8 divided by estimated population number of same ages.

	Age (yr)				Exploitation rate
Analysis	1	2	3	4+	(ages 1–8)
Primary (MARMAP) catch matrix					
(M=0.28)					
1972–78	0.007	0.06	0.08	0.15	0.06
1982–86	0.018	0.12	0.19	0.35	0.12
1992–96	0.014	0.10	0.15	0.44	0.16
(M=0.28, zeroes in index treated as missing)					
1972–78	0.007	0.06	0.08	0.15	0.06
1982–86	0.018	0.12	0.19	0.35	0.12
1992–96	0.011	0.08	0.13	0.40	0.14
(M=0.20)					
1972–78	0.010	0.08	0.11	0.20	0.08
1982–86	0.025	0.16	0.24	0.43	0.16
1992–96	0.017	0.12	0.17	0.49	0.19
(M=0.35)					
1972–78	0.005	0.04	0.06	0.11	0.04
1982–86	0.013	0.09	0.14	0.28	0.09
1992–96	0.012	0.09	0.14	0.40	0.14
Alternate catch matrix					
(M=0.28)					
1972–78	0.006	0.04	0.06	0.14	0.05
1982–86	0.017	0.10	0.18	0.42	0.13
1992–96	0.007	0.06	0.27	0.66	0.18

Estimates of benchmarks from simulations

Estimates of MSY, B_{MSY} and F_{MSY} were made from the stock–recruitment model and age-structured simulations (Table 8; Fig. 10). In addition, minimum stock size threshold (MSST), a benchmark recently introduced into U.S. Federal fishery management, was calculated from B_{MSY} as suggested in Restrepo et al. (1998), namely as MSST = (1–M) B_{MSY}, with M = 0.28/yr. Although benchmarks are somewhat sensitive to assumptions examined, sensitivity was small compared with the difference between estimated benchmarks and current status of the stock and fishery (Table 8). For example, estimates of MSY obtained in this way (240–280 t/yr) were similar to recent landings (about

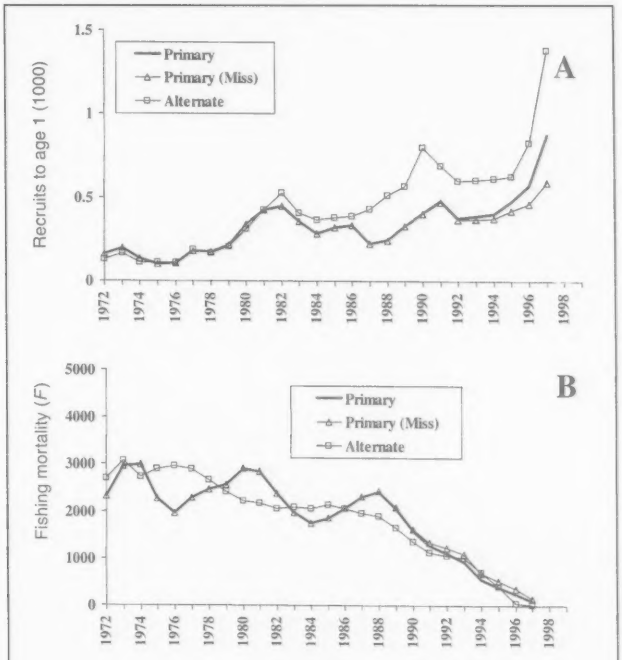

Figure 4

(**A**) Annual estimated instantaneous fishing mortality rates (mean F on ages 4–8), and (**B**) recruitment to age 1 from calibrated VPA applied to red porgy off southeastern United States based on different catch matrices and treatment of zeroes (alternative treatment of zeroes as missing value is indicated as "Miss" after Primary) in MARMAP hook-and-line CPUE.

200–300 t/yr), but well below landings taken earlier (e.g. >800 t in 1981 and 1982). Estimates of fishing mortality rates in the recent period are about 2.7 to 3.6 times those that could produce MSY (Table 8). Because benchmark estimates are based on selectivity patterns estimated for 1992–96, their values are expected to change with the recent introduction of higher minimum size limits. However, the general picture is unlikely to change.

Surplus-production model

It was not possible to estimate the shape parameter of the generalized production model from these data; therefore, we present results only for the logistic model. Fits of that model with various assumptions about B_1/K were statistically equivalent (log likelihoods from –2.29 to –2.25), indicating that the data–model combination is not informative about relative biomass level at the start of the time series. We present results under a range of assumptions centered on $B_1/K = 0.75$ (Table 9). The estimate of MSY was moderately sensitive to the assumption on B_1/K, varying about 18.5% around the central estimate (Table 9); it was also higher than our estimates from age-structured methods (Table 8). Nonetheless, the bias-corrected 80% confidence interval on the central MSY estimate (Table 9) and the corresponding 50% interval (not shown) included the age-structured estimates of MSY; therefore there was some agreement between methods.

Estimates of stock and fishery status expressed in relative terms (Table 9) were similar to those from the age-structured analysis (Table 8) and like those estimates depicted a heavily overexploited stock. Stock biomass at the start of 1998 was estimated as about 25% of the biomass that can support MSY (B_{MSY}), a result that was remarkably insensitive to the assumption on B_1/K. Fishing mortality rate in 1997 was estimated as about twice the fishing mortality rate associated with MSY (F_{MSY}), a result only slightly sensitive to the assumption on B_1/K. Equilibrium yield available in 1998 was estimated as about 44% of MSY; this reduction was due to the stock's reduction well below B_{MSY}.

Estimates of relative stock and fishery status over time displayed a pattern of increasing fishing mortality rate and decreasing abundance over time (Fig. 11). It appears that the biomass moved below B_{MSY} in about 1982 and that the fishing mortality rate has been above F_{MSY} since about 1978. Estimated confidence intervals on F/F_{MSY} are remarkable in encompassing a wide range that since

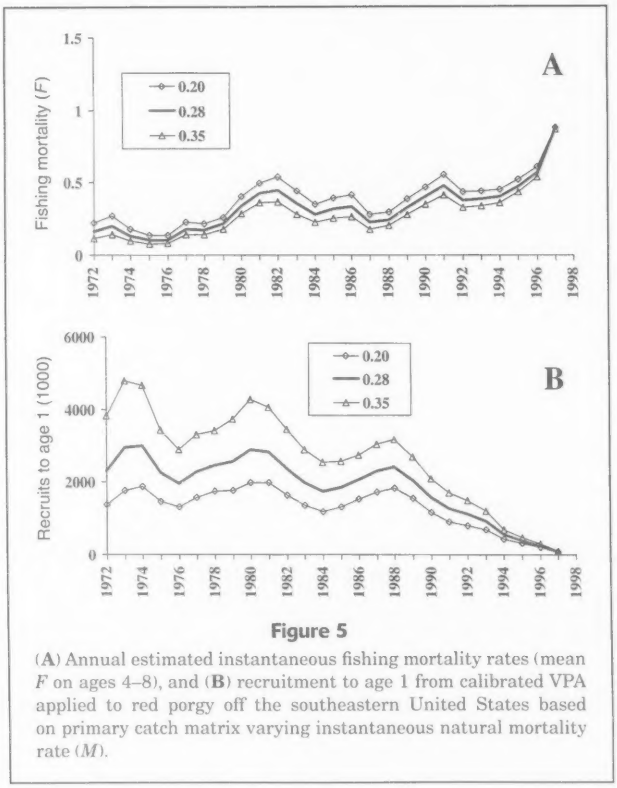

Figure 5

(**A**) Annual estimated instantaneous fishing mortality rates (mean F on ages 4–8), and (**B**) recruitment to age 1 from calibrated VPA applied to red porgy off the southeastern United States based on primary catch matrix varying instantaneous natural mortality rate (M).

about 1980 has included only values greater than unity (Fig. 11B).

Discussion

This work includes numerous advances from previous assessments (Vaughan et al., 1992; Huntsman et al.[1]). The major improvements are availability of additional fishery-dependent and fishery-independent aging data and of fishery-independent indices for calibrating VPAs. Other changes include expanded geographic range, new estimates of sex ratios and maturity schedules, new growth parameters, application of a more modern algorithm for calibrated VPA, and application of a nonequilibrium surplus-production model. Our conclusions agree with both earlier assessments in finding a population in decline.

Because unbiased sampling of wild fish stocks is extremely difficult and fishery data sets are small (in number of years of data), fish population models are not precise approximations of reality. Accurately characterizing uncertainty in assessment results is difficult or impossible: although statistical estimates of uncertainty can be obtained, it is not known how to balance them against factors that tend to increase certainty, such as agreement among data sources or methods and among assessments conducted over time. Any formal estimate of uncertainty in the present assessment results would be large. Nonetheless, in light of our use of complementary models, several independent data sources, and two largely independent sets of age-length keys, and based on agreement with past assessments, we believe that the present results are unequivocal in their major finding of a severely depleted population.

By using two treatments of observed zeroes in CPE series, we illustrated that some results can be sensitive to the method used to treat zeroes. Although addition of a constant before logarithmic transformation is a widely used practice and has been a common statistical recommendation (e.g. Snedecor and Cochran, 1980; Berry, 1987), it is becoming evident that the practice can be problematic in estimation of abundance indices. Logarithmic transformation is made under the assumption of lognormally distributed data, and presence of zeroes in itself violates that assumption. Moreover, results can depend strongly on the additive constant chosen (Porch and Scott, 1994; Ortiz et al., 2000). The root of the problem is that transformed zeroes are usually extreme values in the data set and thus highly influential. Several other statistical models have been proposed, of which the most promising in this application may be the delta–lognormal model (Lo et al., 1992; Ortiz et al., 2000). However, this is still an active area of methodological research, and the matter remains unresolved. We thus used two treatments of zeroes and have

Table 6

Static yield per recruit (YPR) and spawning potential ratio (SPR) of red porgy off southeastern United States. Estimates are based on mean age-specific fishing mortality rates from calibrated VPA on primary or alternative catch matrices (see text), are made under several assumptions about natural mortality rate, M, and treatment of missing values in hook-and-line abundance index, and use selectivity for most recent time period, (1992–96).

Analysis	YPR (g)	Spawning potential ratio				Percentage of males in relation to no fishing[1]
		Total	Female	Eggs	Male	
Primary (MARMAP) catch matrix						
(M=0.28)						
1972–78	152.3	61	74	67	49	83
1982–86	214.3	40	58	47	26	71
1992–96	162.2	42	59	49	27	69
(M=0.28, zeroes in index treated as missing)						
1972–78	152.3	61	74	67	49	83
1982–86	214.2	40	58	47	26	71
1992–96	160.9	44	61	51	29	70
(M=0.20)						
1972–78	263.5	43	60	49	33	74
1982–86	306.6	25	43	31	15	61
1992–96	229.5	29	47	37	17	60
(M=0.35)						
1972–78	89.8	74	84	78	63	89
1982–86	149.5	54	69	60	39	78
1992–96	118.7	52	67	58	36	75
Alternate catch matrix						
(M=0.28)						
1972–78	145.1	64	77	70	53	84
1982–86	261.4	33	53	37	20	69
1992–96	198.2	27	46	33	14	64

[1] Percent relative reduction in numbers of mature males between fished and unfished conditions; i.e. proportion of males under fished conditions is x% of proportion of males under unfished conditions.

presented both sets of results, which are different, but not remarkably so.

Several issues arise from choosing as "primary" the catch matrix developed from fishery-independent age data and as "alternate" the matrix from fishery-dependent data. The choice was by necessity somewhat subjective, but was based on the long-term (1979–94), continuous nature of the fishery-independent data on age at size and its larger sample sizes, in contrast to the intermittent age sampling in the fishery, which required frequent interpolation of age-length keys to construct the alternate catch matrix. The different selectivity of the fishery-independent gear should not significantly bias the primary catch matrix, but fishery-independent samples at larger sizes were sometimes very small, making it necessary to pool data across longer periods for the largest sizes. Parallel analyses were conducted with the two catch matrices to determine sensitivity of major results to the choice of matrices as primary and alternate.

Size selectivity of the gear can have much greater effect in fitting growth models. Fishery-dependent sampling, by selecting larger fish, may overestimate mean size at younger ages, but estimate L_∞ more accurately, whereas fishery-independent sampling, by selecting smaller fish, may underestimate L_∞. In a simulation study, Goodyear (1995) noted: ". . . samples drawn from size-selective gears or fisheries yield biased estimates of mean length at age. . . . Even slight changes in sampling protocol can result in misleading temporal shifts of estimates of size at age." This aspect of the differing selectivity between gears seems important to us, and it can bias estimation of growth models. As a result, we cannot say whether estimated temporal differences in size at older ages result from changes in growth patterns in response to long-term overexploitation (Harris and McGovern, 1997) or from a change in sampling-gear selectivity in the fishery-independent sampling gear (Potts et al., 1998).

Despite questions about size at age over time, patterns of population benchmarks and stock status estimated from

Table 7

Potential biological reference points developed from static yield per recruit (YPR) and spawning potential ratio (SPR) analyses for red porgy off southeastern United States estimated from output from calibrated VPA using selectivity for most recent time period (1992–96), and based on primary catch matrix (three levels of M, and run with missing value for 0.0 in parentheses) or alternate catch matrix (M=0.28). See text for derivation of catch matrices.

	Primary catch matrix				Alternate catch matrix
	M=0.20	M=0.28	M=0.28 (missing)	M=0.35	M=0.28
Yield per recruit (YPR) analysis					
$F_{0.1}$	0.15	0.23	(0.23)	0.31	0.25
F_{max}	0.25	0.53	(0.56)	0.84	0.72
Static spawning potential ratio analysis (static SPR)					
Female (eggs)					
F_{30}	0.25	0.49	(0.50)	0.79	0.77
F_{35}	0.20	0.37	(0.38)	0.60	0.55
F_{40}	0.17	0.29	(0.30)	0.46	0.41
Total spawning-stock biomass					
F_{30}	0.25	0.42	(0.43)	0.69	0.51
F_{35}	0.20	0.33	(0.34)	0.52	0.38
F_{40}	0.17	0.26	(0.27)	0.40	0.30
Observed full F by period					
1972–78	0.20	0.15	(0.15)	0.11	0.14
1982–86	0.43	0.35	(0.35)	0.28	0.42
1992–96	0.49	0.44	(0.40)	0.40	0.66

Table 8

Parameters and potential biological reference points developed for Beverton-Holt spawner-recruit model of red porgy off southeastern United States. Estimates are based on calibrated VPA by using selectivity for most recent time period (1992–96), and based on primary catch matrix (fishery-independent keys; includes separate run with missing value for zeroes in hook-and-line index) or alternate catch matrix (fishery-dependent keys).

Parameter estimate or reference point	Primary catch matrix	Primary CM (missing)	Alternate catch matrix
Parameter estimates (standard error in parentheses)			
b_0	1.83×10^{-4}	2.01×10^{-4}	2.32×10^{-4}
	(7.0×10^{-5})	(6.7×10^{-5})	(5.3×10^{-5})
b_1	0.669	0.617	0.605
	(0.185)	(0.175)	(0.157)
$\max\{R_1\} = 1/b_0$	5.46×10^6	4.98×10^6	4.31×10^6
Reference points			
MSY	242	248	277
F_{MSY}	0.14	0.15	0.18
B_{MSY}	2564	2425	2387
MSST	1846	1746	1719
Estimates of SSB (spawning stock biomass) by period			
1972–78	2884	2885	3367
1982–86	2326	2330	2651
1992–96	876	953	669
Estimates of stock status			
$F_{92\text{-}96}/F_{MSY}$	3.2	2.7	3.6
$B_{92\text{-}96}/B_{MSY}$	0.34	0.39	0.28

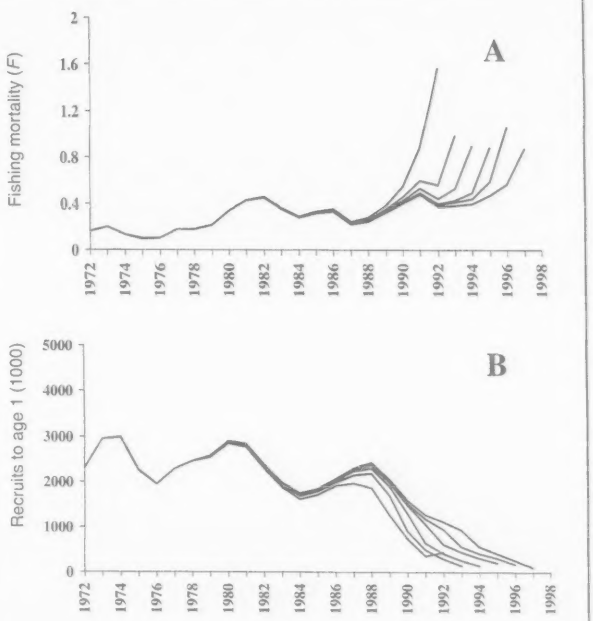

Figure 6

Retrospective patterns in (**A**) annual estimated instantaneous fishing mortality rates (mean F on ages 4–8), and (**B**) recruitment to age 1 from calibrated VPA applied to red porgy off southeastern United States based on primary catch matrix with earlier final year compared to analysis with the most recent final year (1997).

Table 9

Estimates of biological benchmarks and stock status from application of logistic surplus-production model to red porgy off the southeastern United States. Symbols are B_1 = biomass in first year; K = carrying capacity; MSY = maximum sustainable yield; B_{98}/B_{MSY}= biomass at start of 1998 (year following analysis) relative to biomass at MSY; F_{97}/F_{MSY} = fishing mortality rate in 1997 compared with F at MSY; Ye_{98} = equilibrium yield available in 1998. Because B_1 could not be estimated with any precision, the model was fitted under a range of assumptions on its value in relation to that of K. For central case, 80% confidence intervals are shown in parentheses.

Benchmark or status indicator	Assumed value of B_1/K				
	0.55	0.65	0.75	0.85	0.95
MSY (t/yr)	506	482	459 (98–555)	437	416
B_{98}/B_{MSY}	0.247	0.247	0.248 (0.116–0.373)	0.250	0.252
F_{97}/F_{MSY}	1.85	1.93	2.01 (1.36–5.08)	2.09	2.17
Ye_{98} (t)	219	209	199 (69.0–304)	191	183
Ye_{98}/MSY	0.434	0.433	0.434 (0.219–0.607)	0.437	0.440

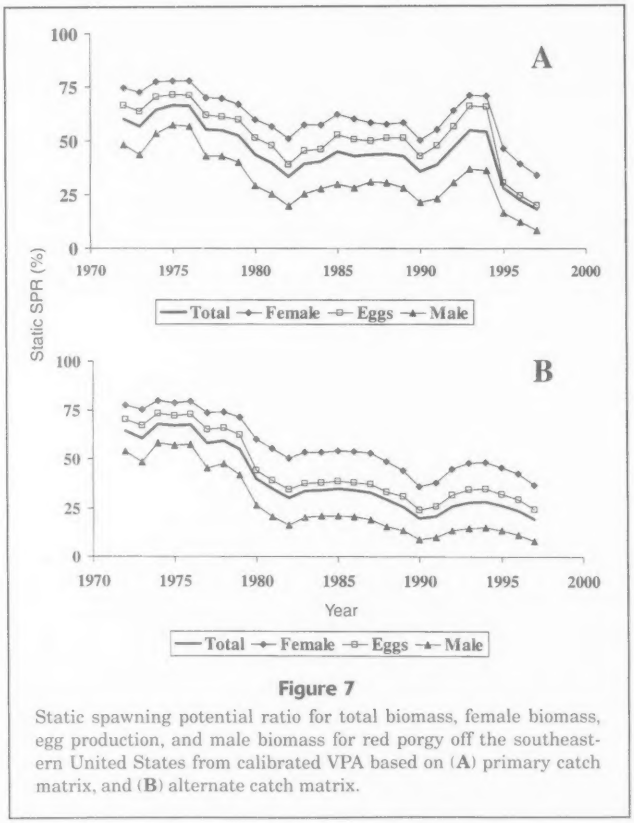

Figure 7

Static spawning potential ratio for total biomass, female biomass, egg production, and male biomass for red porgy off the southeastern United States from calibrated VPA based on (**A**) primary catch matrix, and (**B**) alternate catch matrix.

the two matrices (and, indeed, in all sensitivity runs) were similar, depicting much higher population size and spawning biomass during the 1970s and severe decline through the 1980s and 1990s. This pattern was independent of the large retrospective pattern in the terminal year. Declining trends in CPE from headboats and in fishery-independent sampling (Fig. 3), combined with the observed decline in recruitment (Fig. 4B), also depict an increasingly depleted population. Additional evidence is provided by the surplus-production model, which estimated that the population was at high levels during the 1970s, but that since the mid 1980s it has been far below the level capable of producing MSY (Fig. 11). Implementation of a 12-inch minimum size limit in 1992 (amendment 4 [SAFMC[5]]) appears to have reduced F only on ages 1–3, but F on fully recruited ages (4+) has increased (Table 5).

Static SPR (in total mature biomass) is estimated for the recent period at 42% and 27% from the primary and alternate catch matrices, respectively (Table 6). Mean SPR estimated from the primary catch matrix for all three periods is above SPR=35%, the value used by the South Atlantic Fishery Management Council to define overfishing for red porgy (amendment 12 [SAFMC[3]]). Estimated SPR from the alternate catch matrix is below 35% in the recent period (Table 6).

Coleman et al. (1999), in a discussion of reef fish management, pointed out that SPR as usually estimated from female biomass or egg production has proven less effective for protogynous reef fishes than for fishes that do not change sex. With the loss of the largest size classes, predominantly male, remaining males may not be able to increase harem size sufficiently to fertilize all available females. Thus, determining SPR solely on female reproductive contribution may not capture the true decline in reproduction caused by fishing. For that reason, Vaughan et al. (1992, 1995) recommended calculating static SPR from total mature biomass, broadening the concept of static SPR for protogynous species. Vaughan et al. (1995) calculated reduction in the proportion of males for black sea bass due to changes in fishing mortality and under the assumption that transition rate does not change with population abundance. They estimated a reduction of about 40% due to recent fishing mortality, a reduction similar to the ~30% we estimated for red porgy.

Whether males are currently limiting, or the degree to which increased fishing mortality can cause them to become limiting, is unknown. Regardless, increased fishing mortality on all ages would be expected to reduce the proportion of males in the mature population. The rate at which the imposition of fishing mortality may alter the av-

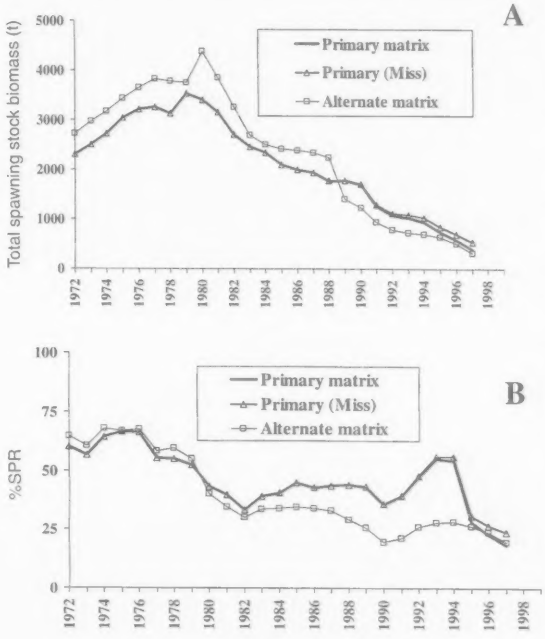

Figure 8

Annual estimates of (**A**) total spawning stock biomass, and (**B**) static spawning potential ratio (SPR) for red porgy off the southeastern United States from calibrated VPA based on different catch matrices and treatment of zeroes (alternative treatment of zeroes as missing value is indicated as "Miss" after Primary) in MARMAP hook-and-line CPUE.

erage age of transition to male is unknown, as is the effect of population density on transformation rate.

Increased sex transformation due to reduced abundance of males, as reported in other protogynous reef fish (Shapiro, 1979), would cause declines in mature female biomass and egg production beyond those expected from fishing alone. McGovern[7] found a greater percentage of males in smaller size classes in 1991–99 than in 1979–81 and suggested that red porgy have compensated for the loss of large individuals by becoming male at smaller sizes. If so, a smaller change in sex ratio, but a greater reduction in egg production, would be expected than implied by increasing fishing mortality alone.

New evidence suggests that red porgy are indeterminate, serial spawners (Daniel[8]). That is, the size and number of batches of eggs are not fixed at the start of the spawning season, but older, larger females spawn in larger batches, more frequently, and possibly over a longer season than younger, smaller females. If so, SPR based on egg production estimated from a fixed weight–fecundity relationship would be unrealistic, and SPR based on total mature biomass would underestimate the contribution of older fish, and thus underestimate the effects of fishing.

Huntsman and Schaaf (1994) proposed accounting for sex-composition changes by multiplying total egg production by a factor representing the probability of successful fertilization. They calculated that probability (Q) for a given fishing mortality rate F^* from the relative change in male contribution of spawning products under fishing:

$$Q = \frac{(G_m / G_f) \mid F = F^*}{(G_m / G_f) \mid F = 0},$$

where G_m and G_f = the gamete contributions of males and females, respectively.

Huntsman and Schaaf (1994) computed G_m as total male biomass and G_f as total female egg production. When new information on red porgy batch spawning becomes avail-

[7] McGovern, J. C. 2001. Personal commun. South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, SC 29422.

[8] Daniel, E. A. 2001. Personal commun. University of Charleston, Charleston, SC 29424.

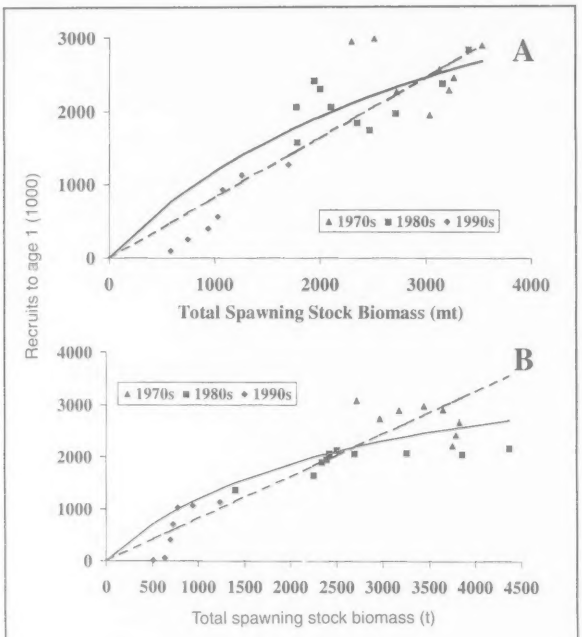

Figure 9

Total spawning-stock biomass and recruitment to age 1 for red porgy off the southeastern United States from calibrated VPA based on (**A**) primary catch matrix, and (**B**) alternate catch matrix. Solid lines represent recruitment predicted from Beverton-Holt models; dashed lines run from the origin with slope of median of recruits divided by the spawning-stock biomass for 1972–94 spawning years.

able and allows calculation of total population fecundity at Z and M, we recommend exploring that approach. Population simulations for a protogynous grouper (Huntsman and Schaaf, 1994) suggest greater vulnerability to fishing than for a comparable gonochoristic stock. It appears that the questions of what SPR measure is most appropriate and how it should be computed cannot be answered until the overall reproductive biology of the species is far better understood.

As usual for fish populations, the spawner–recruit relationship is only roughly defined by the data (Fig. 9), and the years in which the model does not fit raise interesting questions. In the fit based on the primary catch matrix (Fig. 9A), the two large residuals at the start might be taken as suggestive of a dome-shaped recruitment curve, they simply might reflect random error, or they might result from the additional computations needed to extend the catch matrix back to 1972. The analysis based on the alternate catch matrix (Fig. 9B) shows a more pronounced pattern, in which data from the 1970s demonstrate higher recruitment for a given level of spawning-stock size than later data. This pattern might be taken as evidence of a regime shift (change in underlying ecological conditions, from natural or anthropogenic causes), or it might be an artifact of the smaller data sets of age-length data used in this approach. Other explanations are equally possible for residual patterns in Figure 9, A and B. These observed data suggest "depensation" (reverse compensation;decreased, rather than increased, recruitment per spawner at lower population sizes) at very low spawning biomasses, but this suggestion is uncertain because of high retrospective error in estimating recruitment in the most recent years.

Growth overfishing was not estimated to be severe. Mean full F in the early period was estimated well below both F_{max} and $F_{0.1}$. Mean full F in the middle period was estimated as about 152% of $F_{0.1}$, and mean full F for the recent period was estimated as about 191% of $F_{0.1}$, both below F_{max} (Table 7). This stock appears to be one in which recruitment overfishing can be induced before growth overfishing, and for that reason reference points such as F_{max} and even $F_{0.1}$ would be insufficiently conservative for its management.

The estimate of B_{MSY} computed from the recruitment model and selectivity vector can be an appropriate target biomass for management and the corresponding MSST can be a threshold to define overfished status (Restrepo et al., 1998). Estimates of spawning-stock biomass were well above MSST, 1972–78; approached MSST, 1982–86; and were well

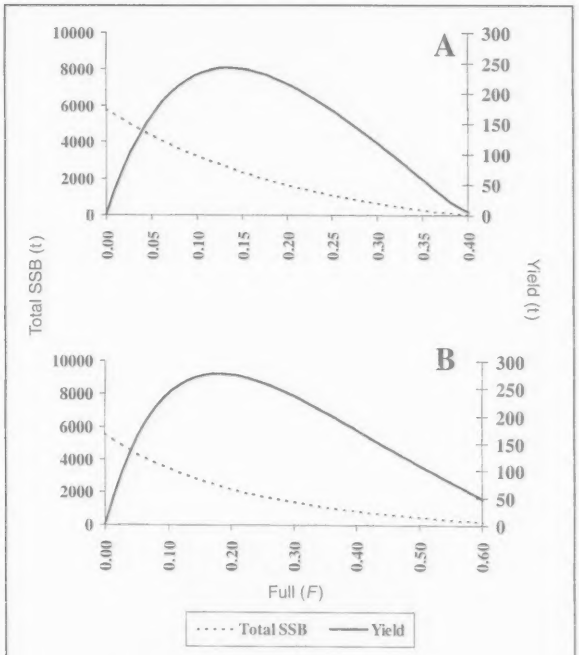

Figure 10

Sustainable yield and spawning stock biomass at varying levels of fishing, projected for red porgy off the southeastern United States from selectivity pattern estimated for 1992–96. Selectivity pattern estimated through calibrated VPA of (**A**) primary catch matrix, (**B**) alternate catch matrix.

below MSST, 1992–96 (Table 8). Still lower estimates of spawning-stock biomass were obtained for the terminal year, although we view terminal-year estimates with scepticism because of retrospective patterns. The production model, not commonly subject to such retrospective patterns, also estimates current biomass as well below MSST (Table 9).

Current estimates of full F (Table 5 for 1992–96) are considerably higher than estimates of F_{MSY} (Tables 8 and 9). In addition, estimates of F_{MSY} are considerably lower than F values corresponding to static SPR of 30% to 40%. If static SPR is used as a reference point, a value higher than SPR = 40% will be necessary to maintain the stock at reasonably productive levels.

It seems inescapable that heavy fishing mortality has been a major cause of the decline in recruitment (Fig. 4B), particularly in the late 1970s and 1980s. Although fishing mortality was lower in the mid-1980s, it increased again in the 1990s for fully-recruited ages (Fig. 4A), and thus static SPR has also declined (Fig. 7). Patterns of increasing F and declining SPR are even more pronounced in estimates from the alternate catch matrix (Figs. 4A, 7). Even though spawning-stock biomass remained high in the late 1970s, recruitment began to decline (Fig. 9). This finding suggests that the usual effects of heavy fishing pressure may have been compounded by other population-specific factors (e.g. those relating to sex structure) or extrinsic factors (e.g. unfavorable environmental conditions) affecting the reproductive success of the population.

Management of hermaphroditic reef fishes is difficult, and it has had few successes (Coleman et al., 1999). As we have shown, interaction of a population's size and sex structures complicates the attempt to model reproductive capacity (e.g. SPR) as a function of fishing mortality rate. Size limits can have subtle side effects if they result in a deficit of males and if larger females in the population consequently change sex at a higher rate. Use of bag limits and size limits in management makes it likely that fish will be caught and released, imposing discard mortality that is incompletely observable. Discard mortality has been found an important factor in collapse of at least one fish stock (Myers et al., 1997). Fish that aggregate become more catchable (increased catchability coefficient $q = F/f$) as abundance declines, another phenomenon associated with risk of collapse (Clark, 1974; Gulland, 1975). Ludwig (1998) has suggested on theoretical grounds that the best management strategy for stocks that may collapse is rapid adjustment of harvest size in response to changes in stock abundance. Ludwig noted: "It is noteworthy that the com-

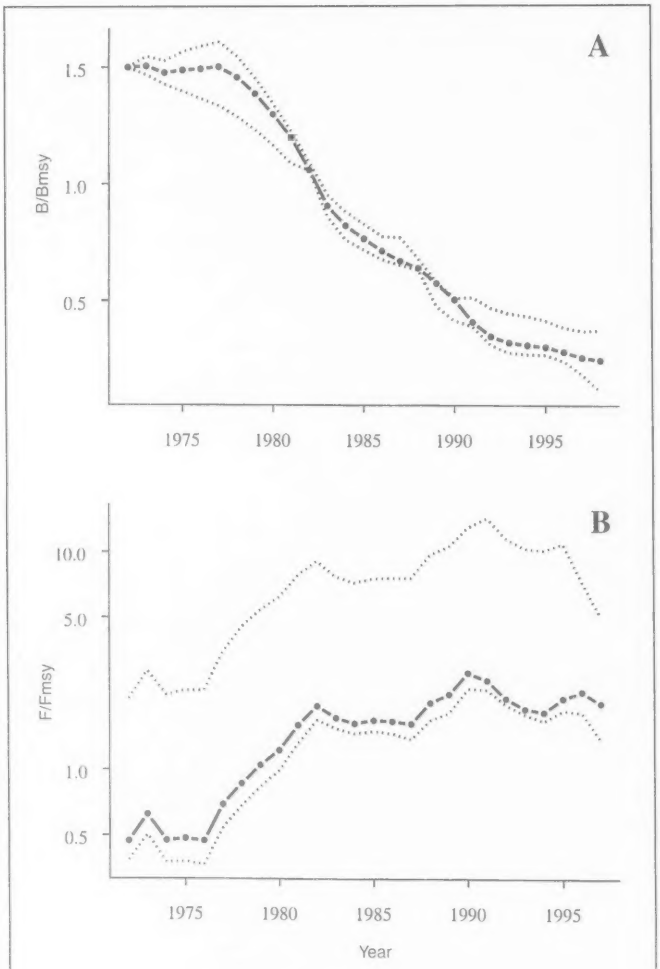

Figure 11

Time trajectories of (**A**) relative population biomass (B/B_{MSY}) and (**B**) relative fishing mortality rate (F/F_{MSY}; log scale) estimated from non-equilibrium logistic surplus production model of red porgy off the southeastern United States under assumption $B_1/K = 0.75$. Dotted lines are 80% confidence intervals from bootstrapping.

plications in stock dynamics all have the same effect upon performance of [management] strategies: they all may cause drastic increases in the probability of extinction and decreases in the expected discounted total yield." It was in the face of such difficulties and uncertainties that the concept of precautionary management was developed (FAO, 1995).

In conclusion, as of 1997 the stock of red porgy off the southeastern United States appears to be in poor condition and getting worse. Even after allowing for retrospective patterns and regardless of catch matrix, estimates are of long-term declines in spawning-stock biomass, recruitment, and catch per effort in the headboat fishery and in fishery-independent surveys. Such estimates strongly suggest overexploitation—overexploitation at an unsustainable rate. Static SPR since 1985 has generally been above the present criterion for overfishing (SPR > 35%), based on estimates from our primary catch matrix. (Estimates from the alternate catch matrix are lower, and estimates from that matrix are generally even more pessimistic about stock status.) During that period, recruitment and spawning stock have continued to decline. Given the present low population level and poor recruitment, we believe that substantial reductions in fishing mortality rate will be necessary to re-

build the stock, whether or not factors other than fishing have contributed to the decline. The situation may be analogous to that of striped bass (*Morone saxatilis*) off the U.S. Atlantic coast in the 1980s, a population that was extremely depressed, with landings reduced by about 75% from their peak. Models of that decline suggested that sharp reductions in fishing mortality would increase the population's growth rate, regardless of the relative importance of fishing and environmental conditions in the preceding decline. Under vigorous management (with sharp reductions in fishing mortality) the population has made a remarkable recovery (Richards and Rago, 1999).

Since completion of this assessment, the South Atlantic Fishery Management Council has taken several actions to promote recovery. As noted in amendment 12 (SAFMC[3]), amendment 9 to the FMP increased the red porgy minimum size limit to 14-inch total length, established a bag limit of 5 fish per person per day, prohibited purchase or sale of red porgy during March and April, and restricted commercial harvest to the recreational bag limit during those months. Subsequently, a prohibition on landing red porgy (moratorium) was enacted for the period 8 September 1999 through 28 August 2000. Amendment 12 (SAFMC[3]) to the FMP, which became effective on 29 August 2000, reduces the recreational bag limit to 1 fish per person per day, extends the closed season to 4 months (January–April), and allows a 50-pound trip limit for commercial landings during the remaining 8 months of each year. Furthermore, the maximum fishing mortality threshold (MFMT) was increased from SPR = 30% (amendment 4 [SAFMC[5]]) to SPR = 35% (amendment 12 [SAFMC[3]]). It remains to be seen whether these actions will be sufficient to achieve the recovery of red porgy.

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A nearsurface, daytime occurrence of two mesopelagic fish species (*Stenobrachius leucopsarus* and *Leuroglossus schmidti*) in a glacial fjord

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The northern lampfish (*Stenobrachius leucopsarus*, family Myctophidae) and northern smoothtongue (*Leuroglossus schmidti*, family Bathylagidae) are mesopelagic fishes, defined by their vertical distribution in the mesopelagic zone (200–1000 m) during daylight hours. Northern lampfish range from the Bering Sea to southern California (Shimada, 1948), where their abundance is highest along the continental slope and decreases over the continental shelf. They are the most abundant species in the mesopelagic zone of the Bering Sea (Pearcy et al., 1977; Sobolevsky et al., 1996), the Gulf of Alaska (Purcell, 1996), and the eastern North Pacific Ocean off Oregon (Pearcy, 1964; Pearcy et al., 1977). Northern smoothtongue also concentrate in areas bordering the continental slope and are widely distributed from southern British Columbia to the Bering Sea (Peden, 1981) and are very abundant in the Okhotsk Sea (Sobolevsky et al., 1996).

Although larval myctophids spend day and night in nearsurface waters (Frost and McCrone, 1979), juvenile and adult northern lampfish typically inhabit depths of 300–600 m during the day (Paxton, 1967; Pearcy et al., 1977; Frost and McCrone, 1979; Sobolevsky et al., 1996; Watanabe et al., 1999). Off the Oregon coast northern lampfish exhibit semimigrant behavior: a large portion of the population migrates from a daytime depth of 300–600 m to about 50 m at night, and a nonmigratory portion of the population has both a day- and night-time vertical distribution at about 500 m depth (Pearcy et al., 1977). This semimigrant behavior also occurs in the Gulf of Alaska (Frost and McCrone, 1979), in the western North Pacific off Japan (Watanabe et al., 1999), and off California in both the San Pedro Basin (Paxton, 1967) and Santa Barbara Basin (Cailliet and Ebeling, 1990). After sunset, migratory northern lampfish have been collected at depths as shallow as 20 m in the Bering Sea (Nagasawa et al., 1997). We are unaware of any studies in which adult northern lampfish were collected at depths of less than 100 m prior to sunset.

Northern smoothtongue migrate from the mesopelagic zone (200–1000 m) in the day to the epipelagic zone (0–200 m) after sunset (Sobolevsky et al., 1996). Larval northern smoothtongue are abundant in the upper 50 m of Alaskan coastal waters during daylight (Haldorson et al., 1993; Norcross and Frandsen, 1996), but after the postlarval and early juvenile stages they are typically found at depths greater than 150 m (Taylor, 1968; Mason and Phillips, 1985). Previous accounts of adult northern smoothtongue at shallow depths were those of collections made after sunset (Barraclough, 1967; references in Hart, 1973), and in some areas adults do not exhibit diel vertical migration but remain at depths below 240 m (Mason and Phillips, 1985). There has previously been no documentation of either juvenile or adult northern smoothtongue in the upper 50 m of the water-column prior to sunset. The purpose of our study was to document the nearsurface (<15 m), daytime occurrence of both juvenile and adult northern lampfish and northern smoothtongue in Glacier Bay, Alaska.

Materials and methods

Glacier Bay is a fjord in Southeast Alaska that extends northward and bifurcates into a west arm and Muir Inlet (Fig. 1). We conducted 48 midwater trawl tows at 34 stations from 10 to 23 June 1999. Fishes were located with a Biosonics DT4000 digital 120-kHz echo sounder, and significant targets were fished with a modified herring mid-water trawl with a mouth opening of 50 m^2. Mesh sizes diminished stepwise from 5 cm in the wings to 1 cm at the codend, which was lined with 3-mm mesh. A plastic collecting bucket with 1-mm mesh was attached to the end of the codend, and was detached and rinsed after each tow. A Furuno net-sounding system monitored the depth of the headrope during fishing operations. A temperature depth recorder (TDR, Wildlife computers model MK7) was mounted on the headrope to determine the exact depth of the net during fishing oper-

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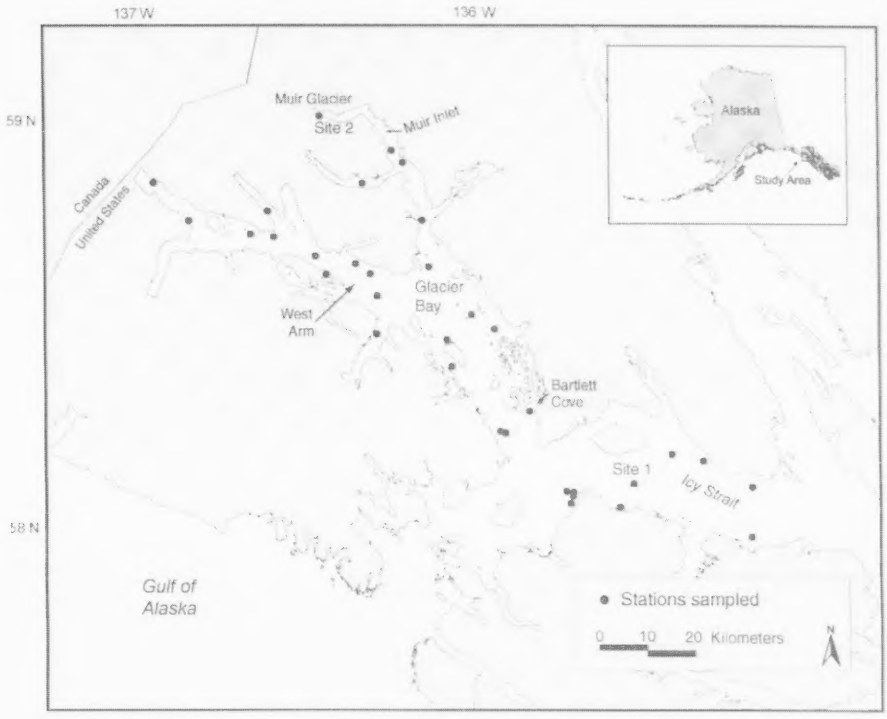

Figure 1

Stations (•) sampled by midwater trawl in Icy Strait and Glacier Bay, Alaska, during June 1999.

ations. Mid-water trawls were considered failures if the trawl doors crossed, the net mesh tore, or if the net-sounding system failed to detect the headrope of the trawl. These tows were omitted from data analysis.

We fished from a 22-m stern trawler, the RV *Pandalus*. The towing speed was about 2.5 kn, and the average tow duration was 20 minutes. There was one deep tow at site 1. At site 2 there were four tows, beginning with three shallow tows and ending with one deep tow to 100 m (Table 1). All fishing was done prior to sunset between 0839 and 1933 h ADT (Alaska daylight time). After fishing at a station, we deployed a CTD (Seabird Electronics Inc, SBE-19 SEACAT profiler) to measure water temperature (°C), salinity (ppt), density (kg/m^3), turbidity (FTU, formazine turbidity units), and chlorophyll concentration (µg/L). CTD measurements were taken every second and we present average values (n=3) of data collected in each 1-m depth interval. If multiple fishing tows were made at a station, only one CTD cast was made.

All fishes were identified in the field to the lowest possible taxon, counted, and fork length (FL) was measured to the nearest millimeter. Length-frequency histograms were plotted for northern lampfish and northern smoothtongue, and fish lengths were grouped in increments of 2 mm. Ages were estimated from length-frequency histograms based on previous studies of length-at-age and length-at-maturity for northern lampfish (Smoker and Pearcy, 1970; Nagasawa et al., 1997) and northern smoothtongue (Mason and Phillips, 1985; Sobolevsky and Sokolovskaya, 1996).

Results

Both mesopelagic species were captured infrequently; northern lampfish were present at only two of the 34 stations (n=60) and northern smoothtongue at only one station (n=133, Table 1). Northern lampfish and northern smoothtongue accounted for only 4% of the 5011 fish captured at all 34 stations; capelin (51%, *Mallotus villosus*) and walleye pollock (36%, *Theragra chalcogramma*) were the most abundant species. Northern lampfish mature at 4 years of age, and of the 60 individuals captured, about 86 % were juveniles (31–59 mm FL) and 14% were adults (65–83 mm FL). Northern smoothtongue mature at 2 years of age, and of the 133 individuals captured, about 64% were juveniles (35–53 mm FL) and 36% were adults (54–85 mm FL, Fig. 2).

At site 1, two individual northern lampfish (sizes 31 and 37 mm) were captured at 90 m depth during daylight (Fig. 1, Table 1). At site 2, next to Muir Glacier, we fished during daylight hours from 1730 to 1930 h. In the first tow (4.5 hours prior to sunset), we fished at 10–15 m depth and 12% of the northern lampfish were adults

Table 1

Station information from the two sites where northern lampfish (*Stenobrachius leucopsarus*) and northern smoothtongue (*Leuroglossus schmidti*) were present. The number of each species captured is given. Listed values of water temperature (°C), salinity (ppt), density (kg/m^3), turbidity (FTU), and chlorophyll concentration (µg/L) are those which correspond to the fishing depth.

		Site 2			
	Site 1	Tow 1	Tow 2	Tow 3	Tow 4
Northern lampfish (no.)	2	57	0	0	1
Northern smoothtongue (no.)	0	81	0	0	52
Region	Icy Strait	Muir Inlet	Muir Inlet	Muir Inlet	Muir Inlet
Date	6/12/99	6/15/99	6/15/99	6/15/99	6/15/99
Time of day	1540	1730	1830	1850	1930
Time prior to sunset (hour: min)	6:23	4:36	3:36	3:16	2:36
Latitude (North)	58° 16.28′	59° 04.27′	59° 04.13′	59° 03.95′	59° 04.44′
Longitude (West)	135° 37.38′	136° 19.93′	136° 19.07′	136° 19.07′	136° 19.59′
Bottom depth (m)	124	187	187	187	187
Fishing depth (m)	90	10-15	10	20	100
Temperature (°C)	5.77	5.18	5.69	4.83	4.28
Salinity (ppt)	32.07	30.37	29.70	30.73	31.15
Density, sigma-theta (kg/m3)	25.29	23.99	23.40	24.31	24.69
Turbidity (FTU)	8.09	14.97	15.14	14.67	11.69
Chlorophyll concentration (µg/L)	1.61	1.38	2.15	1.30	0.86

and 88% were juveniles. At 100 m (tow 4) only one northern lampfish (44 mm FL) was captured. Northern smoothtongue were also captured at depths of both 10–15 m (tow 1) and 100 m (tow 4), and both catches consisted of 39% adults and 61% juveniles.

Among all stations, oceanic parameters measured at the depth of fishing had the following ranges: temperature (4.3–8.2°C), salinity (26.3–32.1 ppt), density (20.7–25.3 kg/m^3), turbidity (7.3–15.1 FTU), and chlorophyll concentration (0.9 – 25.4 µg/L). Vertical profiles of water temperature (°C), salinity (ppt), and density (kg/m^3) at sites 1 and 2 indicated that the thermocline, halocline, and pycnocline occurred at depths <10 m. The upper 10 m of the water column at site 2 had the lowest average surface salinity (26.3 ppt) and the highest turbidity of any of the 34 stations sampled in our study. Turbidity values at site 2 were >15 FTU from 3 to 16 m and >10 FTU to depths of 41 m; turbidity at site 1 was low and ranged from 7.8 to 8.7 FTU (Fig. 3). At site 2 the maximum chlorophyll concentration (16.1 µg/L) occurred at 5 m; whereas at site 1 the chlorophyll concentration peaked (24.7 µg/L) at 12 m and remained high (>10 µg/L) to 28 m.

Discussion

Prior to sunset, juvenile and adult mesopelagic fishes were found at depths of 10 to 15 m near Muir Glacier in Glacier Bay, Alaska. Diel migrations of northern lampfish may be a response to light intensity (Paxton, 1967; Pearcy et al., 1977) or be stimulated by hunger (Pearcy et al., 1977; Cailliet and Ebeling, 1990). In the spring–summer period, when daylight hours increase in the Bering Sea, vertical migrations of northern lampfish and northern smoothtongue had smaller amplitudes and were not as distinct (Sobolevsky et al., 1996). Phytoplankton blooms and fog banks can reduce the depth to which light can penetrate, also causing northern lampfish to migrate higher in the water column (Barham, 1957).

Turbidity in the upper water layer next to Muir Glacier was higher than anywhere else in this study (15 FTU), and this high turbidity corresponded with the shallowest occurrence of mesopelagic fishes. In contrast, in Icy Strait at site 1, where the turbidity was lower, northern lampfish were captured at 90 m depth during daylight hours (Table 1, Fig. 3). High turbidity from glacial silt at Muir Glacier may significantly reduce light penetration and account for the presence of northern lampfish and northern smoothtongue at 10–15 m depth prior to actual sunset.

Although these mesopelagic fishes are more commonly distributed along the continental slope, both northern lampfish (Shimada, 1948; Taylor, 1968) and northern smoothtongue (Mason and Phillips, 1985) also occur in deep, nearshore waters from the eastern Gulf of Alaska to Puget Sound, Washington. Northern lampfish were observed in Icy Strait and Lower Glacier Bay, Alaska, previously,[1] but not as far inland as Muir Glacier. Northern smoothtongue have not been observed previously in the same area. Their occurrence along the inside waters and fjords of Southeast Alaska makes them available to a suite of predators that otherwise might feed upon them only offshore.

[1] Wing, B. 2000. Personal commun. National Marine Fisheries Service, Auke Bay Laboratory, 11305 Glacier Highway, Juneau, Alaska, 99801.

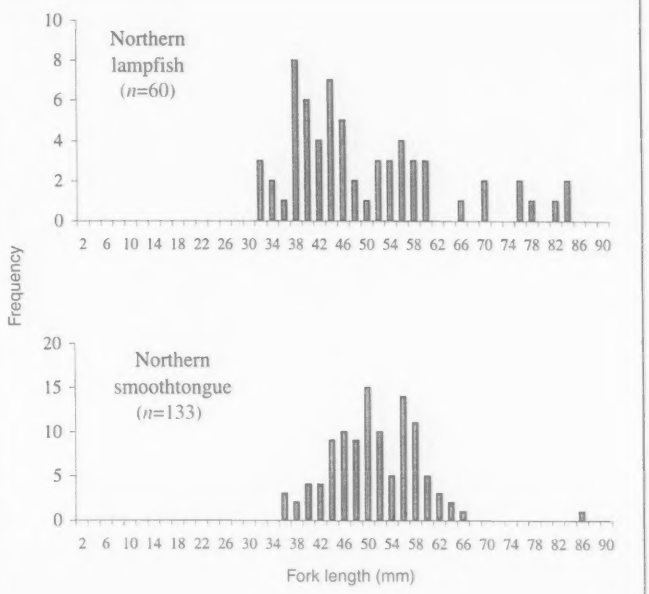

Figure 2

Length-frequency histograms for northern lampfish (*Stenobrachius leucopsarus*) and northern smoothtongue (*Leuroglossus schmidti*). Lengths were grouped in 2-mm intervals. The total number of fish that were measured is given in parentheses.

Northern lampfish and northern smoothtongue serve as important links in oceanic food webs (Cailliet and Ebeling, 1990). Myctophids provide a high-lipid energy source for a variety of predators (Van Pelt et al., 1997; Springer et al., 1999). For example, stomachs of marbled murrelets (*Brachyramphus marmoratus*) collected at the entrance to Glacier Bay contained northern lampfish almost exclusively.[2] Black-legged kittiwakes (*Rissa tridactyla*), which are restricted to foraging on fish at the surface, must feed nocturnally to obtain northern lampfish at oceanic islands in the Aleutians (Springer et al., 1996). However, near Muir Glacier and other tide-water glaciers in Glacier Bay, kittiwakes may be able to regularly forage on myctophids during daylight hours. Further investigations of fish distributions and predator diets are necessary to understand trophic interactions in Alaska's glacial fjords such as Glacier Bay.

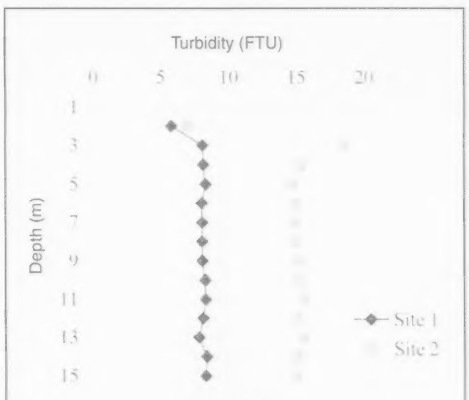

Figure 3.

Vertical profiles of turbidity (FTU, formazine turbidity units) at site 1 and site 2 from the surface to 15 m depth. Black diamonds symbolize data from site 1 and gray squares symbolize data from site 2.

Acknowledgments

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[2] Piatt, J. F. 1991. Unpubl. data. U.S. Geological Survey, 1011 E. Tudor Road, Anchorage, Alaska, 99503.

funds obtained for studies of forage fish in Glacier Bay National Park (GBNP). We thank Jim Taggart (USGS) and Mary Beth Moss (GBNP) for encouragement and logistic support.

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Opportunistic feeding of longhorn sculpin (*Myoxocephalus octodecemspinosus*): Are scallop fishery discards an important food subsidy for scavengers on Georges Bank?

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There has been much recent interest in the effects of fishing on habitat and non-target species, as well as in protecting certain areas of the seabed from these effects (e.g. Jennings and Kaiser, 1998; Benaka, 1999; Langton and Auster, 1999; Kaiser and de Groot, 2000). As part of an effort to determine the effectiveness of marine closed areas in promoting recovery of commercial species (e.g. haddock, *Melanogrammus aegelfinus*; sea scallops, *Placopecten magellanicus*; yellowtail flounder, *Limanda ferruginea*; cod, *Gadus morhua*), nontarget species, and habitat, a multidisciplinary research cruise was conducted by the Northeast Fisheries Science Center (NEFSC), National Marine Fisheries Service. The cruise was conducted in closed area II (CA-II) of the eastern portion of Georges Bank during 19–29 June 2000 (Fig. 1). The area has historically produced high landings of scallops but was closed in 1994 principally for groundfish recovery (Fogarty and Murawski, 1998). The southern portion of the area was reopened to scallop fishing from 15 June to 12 November 1999, and again from 15 June to 15 August 2000. While conducting our planned sampling, we observed scallop viscera (the noncalcareous remains from scallops that have been shucked by commercial fishermen at sea) in the stomachs of several fish species at some of these locations, namely little skate (*Raja erinacea*), winter skate (*R. ocellata*), red hake (*Urophycis chuss*), and longhorn sculpin (*Myoxocephalus octodecemspinosus*). We examined the stomach contents of a known scavenger, the longhorn sculpin, to evaluate and document the extent of this phenomenon.

Fishery discards provide food subsidies that help maintain fish populations, but to what extent is unclear. There is some evidence that fishery discards allow fish populations to be more abundant than they would be with just ambient resources (e.g. Polis and Strong, 1996). Others would counter that these discards may maintain a population but not necessarily lead to population growth (Fonds and Groenewold, 2000). As an extension of our opportunistic field observations from the closed area (CA)-II 2000 cruise, we examined NEFSC historical bottom trawl survey and food-habits databases to ascertain the role of fishery discards in the Georges Bank ecosystem, with particular respect to the longhorn sculpin population.

Materials and methods

Our sampling was conducted concurrently with the scallop fishery, therefore it was necessary to continuously monitor vessel activity in the area opened to fishing prior to our arrival and during our sampling. Prior to sampling, we collected biweekly summaries of scallop fishing vessel activity during the 1999 open season, and day by day summaries of the 2000 season were obtained from the northeast region vessel monitoring system (VMS), National Marine Fisheries Service. With this system, individual vessel locations are transmitted to NMFS every 30 minutes (McSherry[1]). The location of each fishing vessel was plotted (with Surfer 7.0; GSI, 1999) on a map overlaid with the sampling sites occupied during the 1999 study (June 1999). Stations from the 1999 study were chosen on the basis of fleet activity during the 1999 open season and our sampling goals. Each day while the RV *Albatross IV* was in CA-II, current individual scallop-vessel activity data were transmitted to us by email, plotted, and sampling stations were selected after an examination of the data.

As part of our sampling protocol, a 15-minute otter trawl haul was made at each station, towed at a speed of 6.5 km/h. A standardized NEFSC no. 36 Yankee otter trawl rigged with a rubber-disc-covered chain sweep, 11 floats, 5-m ground cables, and 450-kg polyvalent trawl doors (commonly referred to as a "flatfish net") was used. Once the trawl was on deck, we sorted fish and macro-invertebrates by species, weighed each species (0.1 kg), measured lengths of all fish (cm), examined subsamples of the fish to determine sex, maturity, and stomach contents, and collected structures to determine ages. For further details of the survey and food habits methods used in our study see Azarovitz (1981) and Link and Almeida (2000), respectively.

After initial observations of scallop viscera in fish stomachs at several previous locations, we developed an *ad hoc* study that deliberately selected two stations located in areas of high scallop fishing effort and two stations in areas of little or no scallop fishing effort. On 21–22 June 2000 we sampled stations 8B, 7D, 7E, and 8E in the northeast portion of the region open to the scallop fleet (Fig. 1). At stations 8B and 7E, we observed a high frequency of scal-

[1] McSherry, M. 1998. NMFS Northeast vessel monitoring system—operations logic and geographical display interface. NMFS NE Law Enforcement Office Internal Document, 20 p. [Available from NMFS, NEFSC, 166 Water St., Woods Hole, MA 02543.]

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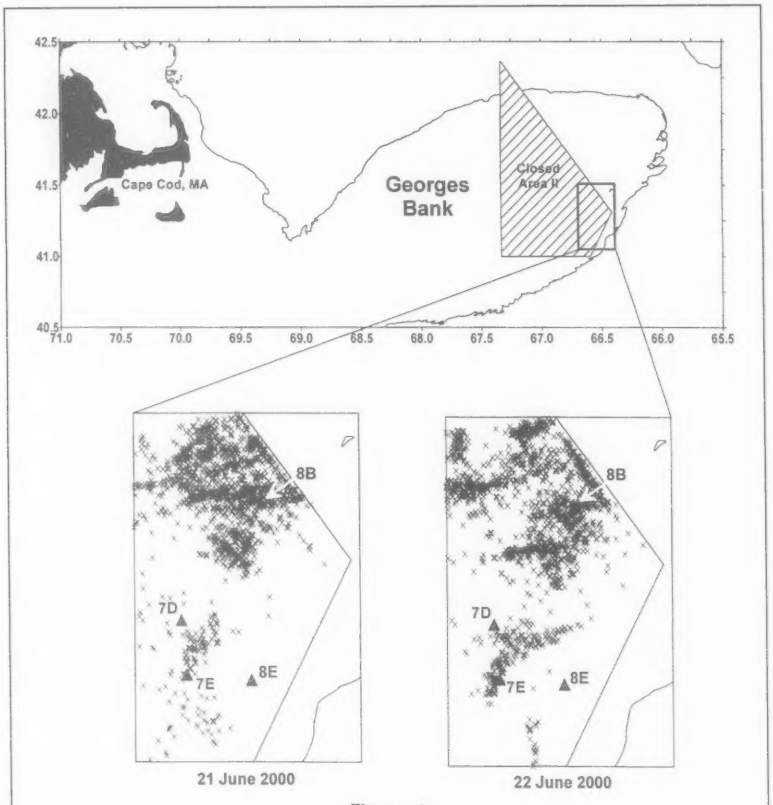

Figure 1

The northeast U.S. continental shelf region, with scallop fishing fleet activity (×) in closed area II of Georges Bank on 21–22 June 2000 overlaid with the sampling sites (▲) occupied by the NOAA FRV *Albatross IV* (Cruise AL 00-03).

lop viscera in the diets of longhorn sculpin, among other species, and undertook extra sampling of sculpin stomachs to assess the magnitude of this phenomenon. We also undertook extra sampling of sculpin at the other two stations. We present mean stomach volume and mean percent (by volume) diet composition for longhorn sculpin at these four stations.

To determine the prevalence of this phenomenon and whether discarded scallop viscera are a regular food subsidy that significantly influences the sculpin population, we examined the stratified mean number of sculpin per tow on Georges Bank (Azarovitz, 1981). We calculated this index of abundance across the fall bottom-trawl survey time series from 1963 to 1998. Additionally, we examined the mean stomach contents (cm^3), maximal stomach contents, percent frequency of occurrence of bivalve, mollusk, or pectinid viscera, and an index of gorge feeding on an annual basis from the food habits time series (Link and Almeida, 2000). The index of gorge feeding (or more simply, the gorge index) was calculated as the percent of stomachs examined with total stomach contents greater than 10 cm^3. We executed a simple linear correlation between the sculpin food-habit metrics and the index of abundance to determine if any significant relationship exists between gorge feeding and sculpin population abundance.

Results

On 21 and 22 June 2000, scallop fishing clearly occurred at stations 8B and 7E, whereas no scallop fishing occurred at 7D or 8E (Fig. 1). Rock crabs (both *Cancer irroratus* and *C. borealis*) and small crustaceans typify the diet of longhorn sculpin (Fig. 2). However, at stations in areas with scallop fishing activity, the diet of sculpin was predominately made up of scallop viscera. Crabs and small crustaceans were still a part of the diet at those stations, but did not comprise as large a percentage as was found at nondredged stations.

The volume of food in sculpin stomachs was also an order of magnitude higher at stations with intense scallop fishing activity (8B=38.7 cm^3 ±6.9; 7E=19.4 cm^3 ±12.7) than at those with no scallop fishing (8E=1.7 cm^3 ±1.4; 7D=0.3 cm^3 ±0.1). When scallop remains were present at

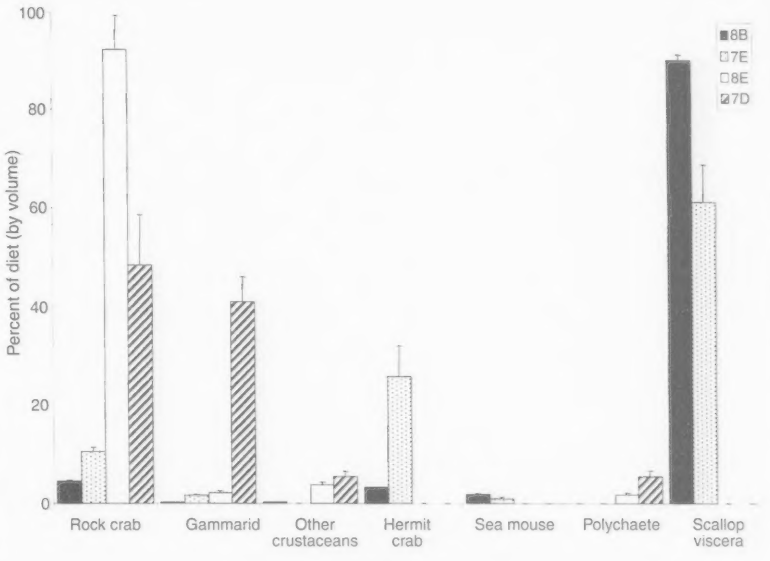

Figure 2

Diet composition (% by volume) of longhorn sculpin at two dredged and two undredged locations in closed area II. Bars are 95% confidence intervals. Sample sizes are 15, 8, 11, 6 fish at stations 8B, 7E, 8E, and 7D respectively.

a location, the amount of food consumed by sculpins increased significantly, suggesting that sculpins continued to feed on crabs and small crustaceans, but opportunistically gorged on the remains of scallops that had been shucked and thrown overboard from scallop fishing vessels operating in the region. Although anecdotal, the stomachs of all sculpins at station 8B, the station most intensely dredged, were distended beyond normal proportions for 20–25 cm fish, often extending below the pectoral fins.

The mean stomach contents of sculpin were effectively constant across the time series, averaging approximately 2 cm^3 (Fig. 3). However, the maximal stomach contents, the percent frequency of bivalve viscera, and the index of gorge feeding showed distinct patterns across the time series. All three of these metrics were generally coincident. Years with a higher gorge index corresponded to years with a high occurrence of bivalve viscera in the diet of sculpins (r=0.70, P<0.01). This finding implies that many, but not all, of the gorging events were on scallop viscera and similar discards. The highest values of the gorge index were observed in 1987 and 1998.

Longhorn sculpin abundance exhibited an initial peak and then a relatively steady period for the first 15 years of the survey, followed by a period of lower abundance during the mid-1980s and an increasing trend in the 1990s (Fig. 4). In most years sculpin abundance ranged from 10 to 20 fish per tow. The years with the highest index of sculpin abundance were 1966 and 1998. In relation to the preceding years, the index of sculpin abundance notably increased during 1966, 1987, and 1998. The latter two years correspond to years when the index of gorge feeding was highest. The correlation between the gorge index and sculpin abundance was weak (r=0.21), but significant and positive (P<0.01).

Discussion

Much of the information describing the impact of fishing gear on benthic communities and habitats has been decidedly negative. It is unclear whether populations of scavengers such as crabs, flatfish, or other demersal fish benefit from indirect effects of fishing (Kaiser and Spencer, 1994; Greenstreet and Hall, 1996; Ramsay et al., 1996) if they are not caught by the fishing gear. It is known that in the short term, scavengers, especially those small enough to fit through the mesh, are attracted to trawl and dredge tracts (e.g. Ramsay et al., 1998; Demestre et al., 2000). Additionally, some studies have actually shown that the abundance of scavenger populations increases in areas that have been trawled (reviewed in Greenstreet and Rogers, 2000). Longhorn sculpin on Georges Bank have maintained their ubiquity and abundance, albeit at relatively low levels compared with other species, during a period of intense fishing pressure in this ecosystem (Fogarty and Murawski, 1998). In recent years the sculpin population on Georges Bank has begun to increase.

Opportunistic feeding on scallop viscera appears to have a positive influence on sculpin populations. The relationship between gorge feeding and sculpin abundance is ad-

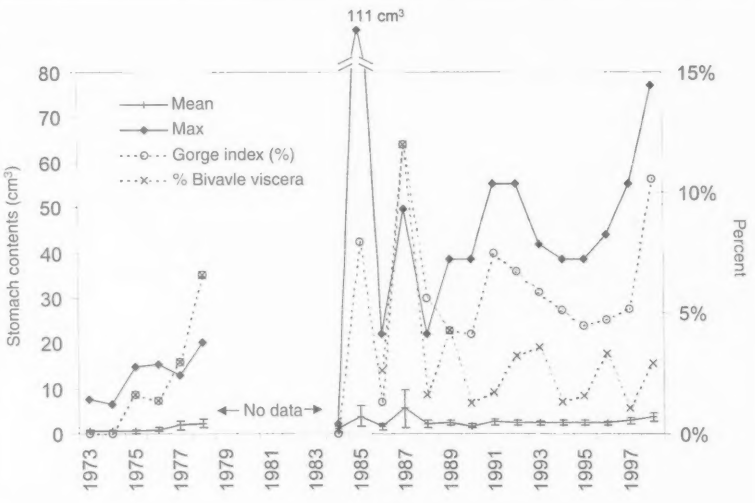

Figure 3

The mean (95% CI) and maximal (largest amount eaten) stomach contents (cm^3) of longhorn sculpin from the NEFSC food habits database. Also, the index of gorge feeding (percentage of stomachs with >10 cm^3) and percentage of stomachs containing bivalve, mollusk, or pectinid viscera.

mittedly weak, yet significant and positive. We recognize that numerous other factors could influence sculpin abundance. However we find it intriguing that the two years with the most drastic increase in sculpin abundance (in the context of recent preceding years; i.e. 1987 and 1996) occurred in years when sculpin gorge feeding was highest.

The amount of food eaten and the diet of longhorn sculpin at stations without scallop fishing activity were similar to those reported for the species on the entire northeast continental shelf (Link and Almeida, 2000) and for Georges Bank in particular (Garrison and Link, 2000). The amount of food eaten and diet at stations with scallop fishing activity showed clear evidence of gorge feeding by sculpin. Other studies have documented opportunistic feeding and changes in diet after groundfish trawling (e.g. gurnards and dabs; Kaiser and Spencer, 1994; Kaiser and Ramsay, 1997), however, this note is the first documentation of scavenging after scallop fishing. The long-term trend shows that, although the average amount of food sculpin consume is relatively constant, the composition of the diet and the frequency of gorging events varies notably. These variations may influence sculpin abundance.

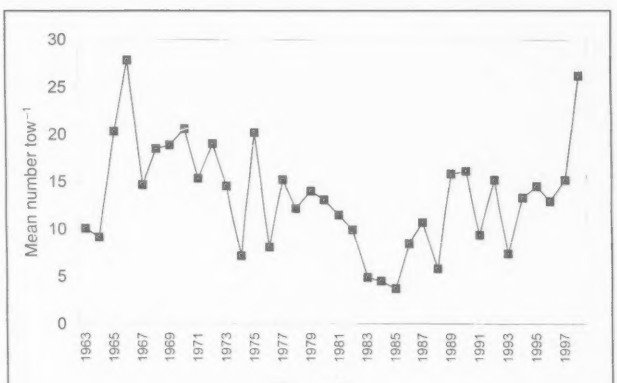

Figure 4

Index of relative abundance of longhorn sculpin from the NEFSC fall bottom trawl survey.

In the 2000 open fishing season in CA-II, more than 760 metric tons (t) of scallop meats were landed (NERO, 2000). If one conservatively assumes that scallop viscera equals the meat weight, then over 760 t (>340,000 lb) of viscera were returned to the southern part of CA-II during this two-month period. The discarded scallop viscera are a relatively small organic input, on an areal basis, to this closed area, which averages ca. 430,000 t in total annual benthic production (111 g/m^2, Cohen and Grosslein, 1987; approximately 3900 km^2 for the southern part of CA-II). How many tons of scallop viscera and similar discards have been deposited across the entire Bank over the past several decades is unknown. Yet, at a local scale scallop viscera may be an important source of energy, akin to similar processes for fish in the deep ocean (Sedberry and Musick, 1978). The biomass of scallop viscera, although

previously a part of the system, is returned in a condition much more readily available to benthic scavengers. Even weak links in terms of diet or energy can be important dynamic links in terms of population regulation (reviewed in Polis and Strong, 1996). The reintroduction of scallop viscera may not be a large addition of energy to the Georges Bank ecosystem, but it may be an important one for sculpin and other opportunist populations.

There is evidence that energy derived from fishery discards can cause scavengers to become more abundant than they would be with ambient resources (Polis and Strong, 1996), or at least these discards can help scavengers maintain population abundance under disturbed circumstances (Fonds and Groenewold, 2000). Further studies may indicate that events which produce food subsidies such as those documented in this study may be more common than generally suspected. Given the ubiquity of naval, commercial, and private vessels on the ocean, it likely that organic waste from these ships, from fishing activities, and from similar processes serves as a significant "rain of food" for benthic scavengers.

Acknowledgments

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First record of a yellowfin tuna (*Thunnus albacares*) from the stomach of a longnose lancetfish (*Alepisaurus ferox*)

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In 1987 we found a juvenile yellowfin tuna, *Thunnus albacares* (Bonnaterre, 1788), in the stomach of a longnose lancetfish, *Alepisaurus ferox* Lowe, 1833. Analysis of published information on lancetfish food habits (Haedrich, 1964, 1969; Haedrich and Nielsen, 1966; Parin, 1968; Parin et al., 1969; Fourmanoir, 1969; Grandperrin and Legand, 1970; Kubota and Uyeno, 1970; Legand et al., 1972; Kubota, 1973; Fujita and Hattori, 1976; Matthews et al., 1977) led us to conclude that this was the first record of a yellowfin tuna found in a lancetfish stomach.

Although this finding has been recorded in "gray literature" (Zamorov et al.[1]; Zamorov and Romanov[2]), the limited circulation of this type of literature, the fact that there were some inaccuracies in the details of the record, and the absence of similar findings in recent studies (Okutani and Tsukada, 1988; Moteki et al., 1993), led us to publish the finding with correct information in the following note.

Materials and methods

A juvenile yellowfin tuna (Fig. 1) in good condition was found in the stomach of a lancetfish caught by pelagic longline on 17 May 1987 during a research cruise in the waters of the exclusive economic zone of Mauritius, western Indian Ocean. The longline set position was 9°32′S, 58°03′E. The depth of hook, which caught the lancetfish, was 99 m.

Results and discussion

The fork length (FL) of the lancetfish was 167 cm, its weight was 9 kg; FL of the yellowfin tuna was 37 cm and its weight was 790 g. The tuna was immature and its stomach was empty. The tuna was 22.2% of the lancetfish body length and 8.8% of its weight. The tuna was found in the lancetfish stomach with its tail towards the mouth of the lancetfish. Evident transverse lateral damage to the tuna body included long, deep, open wounds and an absence of skin and scales in the middle part of the body. Deep wounds were absent on the head and caudal part of the tuna, where damage was minor (Fig. 2). Analysis of the photos allowed us to hypothesize about the manner of capture. Presence of transverse damage to the middle part of the body suggested that the tuna was caught by the lancetfish across the body and held until it lost its ability to swim. The teeth of the lancetfish had also caused cuts, likely inflicted during the convulsive struggle of the tuna to free itself. The absence of wounds in other parts of the tuna's body, in particular on its head, indicated that after the tuna became inactive, it was released from the predator's teeth and swallowed head-first. The proportions of the lancetfish mouth and the victim allowed the tuna to be swallowed whole.

Longnose lancetfish is a common bycatch species on tuna longlines in the study area, the northern stream of the South Equatorial Current, during the survey (April–June 1987) and are caught regularly at depths of 60–120 m. We have found slow-swimming animals in the stomachs of lancetfish (Zamorov et al.[1]; Zamorov and Romanov[2]; Romanov and Zamorov[3]). The diet of lancetfish consists of pelagic crustaceans (Hyperiidae, Portunidae, Amphipoda), cephalopods of the families Onychoteuthidae, some Ommastrephidae (*Ornithoteuthis volatilis*), Cirroteuthidae, Octopodidae, Argonautidae, Cranchiidae, Histioteuthidae, Bathyteuthidae, and mesopelagic fishes (*Sternoptyx diaphana, Paralepis elongata, Omosudis lowei, A. ferox, Antigonia rubescens, Tylerius spinosissimus*) (Haedrich and Nielsen, 1966; Parin et al., 1969; Fourmanoir, 1969; Kubota and Uyeno, 1970; Rancurel, 1970; Fujita and Hattori, 1976; Matthews et al., 1977; Moteki et al., 1993). These are slow-swimming species.[4]

[1] Zamorov V. V., A. M. Amelekhina, and A. A. Rybalko. 1992. On the feeding of *Alepisaurus ferox* Lowe, 1833 in the western Indian Ocean. *In* Fauna and ecology of animals. Proc. Zool. Mus. Odessa State Univ. 1, p. 23–37. Odessa National Univ. (ONU), 2, Dvoryanskaya St., 65000 Odessa, Ukraine. [In Russian.]

[2] Zamorov, V. V., and E. V. Romanov. 1993. New data on feeding of lancetfish *Alepisaurus ferox* Lowe, 1833. *In* Resources of tunas and related species in the World Ocean and problems of their rational utilization, p. 115–116. (Abstracts of the reports presented at first interstate conference "Resources of tunas and related species in the World Ocean and problems of their rational utilization," Kerch 1–5 June 1992). YugNIRO, Kerch. [In Russian.]

[3] Romanov, E. V., and V. V. Zamorov. 2002. Feeding habits of longnose lancetfish (*Alepisaurus ferox* Lowe, 1833) in the western Indian Ocean. Manuscript in preparation.

[4] However, small specimens of the fast-swimming ommastrephid squid *Sthenoteuthis oualaniensis* (Lesson, 1830) (mantle length <10 cm) have been found in the stomachs of lancetfish; the schooling life and common behavior of squids, including periods of slow swimming or passive drift, make them vulnerable to this predator.

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Fish. Bull. 100(2):386–389 (2002).

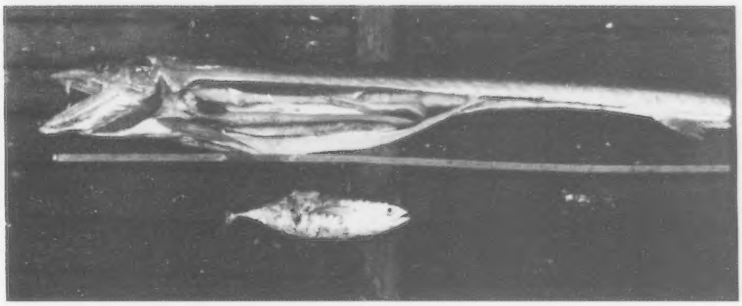

Figure 1
Yellowfin tuna (below) removed from the stomach of the lancetfish (above).

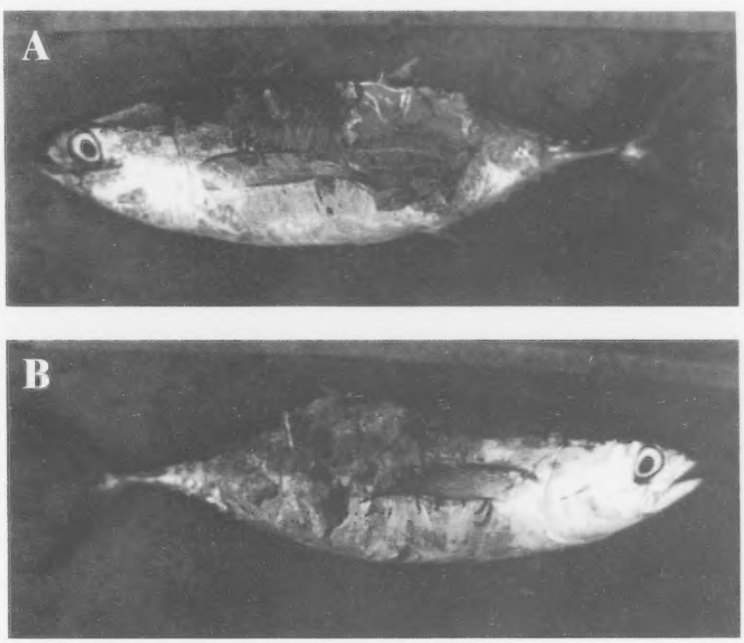

Figure 2
Yellowfin tuna found in lancetfish stomach; viewed from left side (**A**) and right side (**B**).

Studies show that fast-swimming animals, fishes of families Belonidae, Scombridae, Exocoetidae, Carangidae, Coryphaenidae, in particular, and most squids of the family Ommastrephidae, the ordinary food of tunas, are rare or absent in stomachs of lancetfish. Matthews et al. (1977) recorded one case of finding several frigate tunas of the genus *Auxis* in the stomach of one lancetfish, but according to Collette,[5] these were juveniles only 3.9–4.3 cm long. A small (35 cm^3 in volume) juvenile swordfish (*Xiphias gladius*) from a lancetfish stomach was reported by Williams (1967). Large slow-swimming fishes are generally found in the stomachs of lancetfish (Kubota and Uyeno, 1970, Fujita and Hattori, 1976). Cannibalism is also common among lancetfish (Haedrich, 1964; Haedrich and Nielsen, 1966; Fourmanoir, 1969; Matthews et al., 1977; Moteki et al., 1993; Zamorov et al.[1]).

[5] Collette, B. B. 1997. Personal commun. NMFS Systematic Laboratory, National Museum of Natural History, 10th & Constitution Ave. Washington DC, 20560-0153.

Large fast-swimming fish recorded from *A. ferox* stomachs include chub mackerel (*Scomber japonicus*) 35 cm long (Kubota and Uyeno, 1970) and a pink salmon (*Oncorhynchus gorbuscha*) reported by Balanov and Radchenko (1998). However, salmons (*O. gorbuscha, O. nerka,* and *O. keta*) found with slash marks attributed to lancetfish likely indicate that lancetfish also prey on these fast-swimming fish (Radchenko and Semenchenko, 1996).

The jaw structure and large teeth of lancetfish allow these fish to hunt for relatively large animals. However, large epi- and mesopelagic fishes, inhabiting the same or bordering niches with lancetfishes are able to evade attack, as a rule, because of their swimming speeds. The elongate (anguilliform) body of lancetfishes and their flabby and watery muscles suggest an inability to swim for a long time with a high cruising speed in order to chase prey. This species has no developed deep red muscles, a characteristic feature of fishes able to cruise at high speeds (Sharp and Pirages, 1978, He and Wardle, 1988). The muscle tissue of the lancetfish consists mainly of white muscles that are responsible for short-term bursts of motion (Sharp and Pirages, 1978; Schmidt-Nielsen, 1979); and its body form allows it to make short impetuous rushing movements, characteristic of many predatory fishes with anguilliform bodies (Trichiuridae, some of the Gempylidae, Muraenidae, *Anotopterus pharao*, etc.). The high dorsal fin of *A. ferox* and the large area of the caudal fin are additional signs of the high maneuverability of this species for swimming and hunting at short distances.

Yellowfin tuna, unlike lancetfish, are constantly active and swim in a rather fast motion, as has been demonstrated by numerous day-long (or several days long) telemetric tracking experiments (Carey and Olson, 1982; Cayre and Chabanne, 1986; Holland, et al., 1990; Cayre, 1991; Marsac and Cayre, 1998). To maintain hydrostatic equilibrium, small yellowfin tuna swim within the range of 1.3–1.5 body lengths per second (Brill[6]), which in the case of the tuna found in the lancetfish stomach corresponds to a rate of 48–55 cm/s. Rarely the does the speed decrease to 14–22 cm/s (Cayre and Chabanne, 1986, Holland et al., 1990, Brill et al., 1996, Marsac[7]).

Needless to say, it is not easy for a rather slow-swimming lancetfish to catch a fast-swimming tuna. In our opinion, the only way for the lancetfish to catch the tuna was to rush suddenly and to catch the prey with its large saber-like teeth. Ambush-rushing type of hunting is rather widespread among predatory fishes. Perhaps it prevails over other types of prey capture because it is efficient and requires less energetic expense than would an active chase of an escaping victim. In the pelagic environment it is hardly possible to use ambush tactics owing to the character of the pelagic environment, i.e. the absence of natural shelters. Therefore for those fish unable to use high-speed cruise swimming, the method of hunting may be that of lying motionless or slowly sneaking up on the prey and then making a violent rush to catch the prey. For the lancetfish in our study, we suggest that the tuna swam by the motionless or slowly swimming lancetfish at a distance appropriate for a rush but also close enough, so that the tuna was unable to react to or evade the attack.

Obvious lateral damage of the tuna's body may indicate that the lancetfish attacked the tuna in the vertical position either from the belly or from the back. Similar foraging behavior has been suggested for *Anotopterus pharao*, another aulopiform fish that resembles *Alepisaurus* in physical shape and structure, habitat, and diet (Balanov and Radchenko, 1998).

Several of our colleagues suggested that the tuna may have been dead when the lancetfish seized it. Starvation, or if the tunas was a discard from a fishing vessel, and other reasons were given as the cause of mortality. However, in the area of the longline set by the research cruise, and in the general vicinity of the survey, no commercial longline or tuna purse-seine vessels were spotted. We believe that the lancetfish made a successful natural attempt to seize a large, fast swimming food item. If, indeed this was the case, the finding is new and expands our knowledge of lancetfish biology. It also indicates the efficiency of ambush-rushing type of hunting and the ability of a species unable to cruise at high speeds to catch rather large fast-swimming fishes.

[6] Brill, R. W. 1997. Personal commun. Honolulu Laboratory, Southwest Fisheries Science Center, National Marine Fisheries Service, 2570 Dole St., Honolulu, HI 96822-2396.

[7] Marsac, F. 1997. Personal commun. Unité de Recherche n° 109 (THETIS) Centre IRD BP 172 97492 Ste Clotilde Cedex La Reunion, France.

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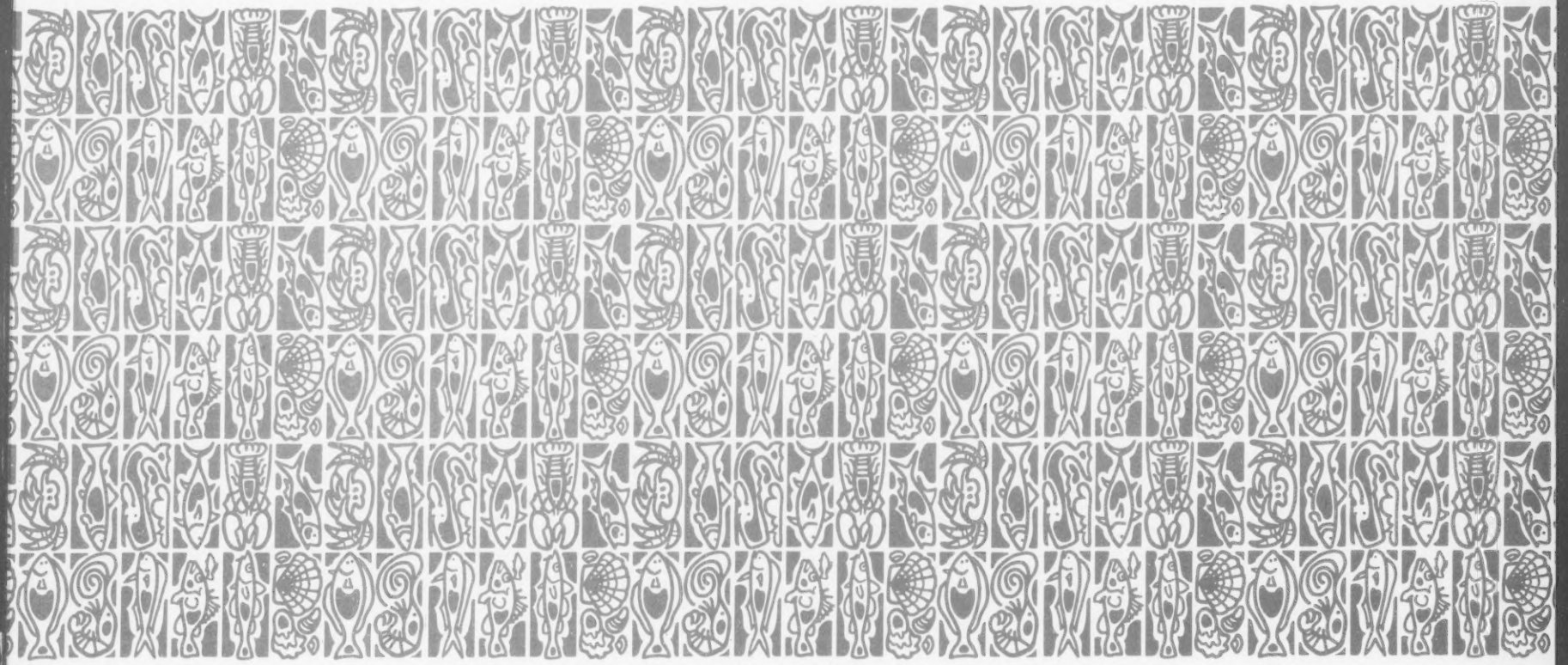
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